

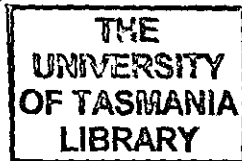
**Attention and Interlimb Coordination: Behavioural and  
Neurophysiological Processes**

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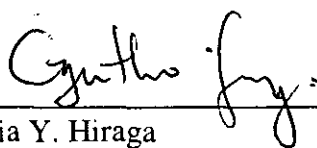
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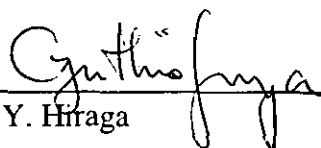


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### **Abstract**

A conceptual and methodological framework has recently been developed from a blending of a traditional dual-task methodology and a dynamical perspective on coordination. Specifically, pattern stability has been shown to be a good predictor of attentional demands (i.e., central cost) needed for maintaining coordination. One of the important assumptions is that the allocation of attentional resources can modify the coupling strength of interlimb coordination. Within this original framework that blends two different theoretical approaches with attention as an intervening variable modifying behavioural patterns, the present research further investigated at the behavioural and neurophysiological levels, the central cost of dynamical coordination patterns.

Two experiments were carried out in the Phase 1 of the present research. The first examined whether previous findings obtained with bimanual coordination patterns could be extended to coordination patterns involving non-homologous limb combinations. Consistent with previous results, coordination stability and probe RT (i.e., a measure of attentional load) were found to co-vary. Furthermore, it was shown that temporal aspects of the coordination task were selectively modulated through attentional prioritisation without affecting the spatial aspects of the task (i.e., movement trajectories).

Following evidence from Experiment 1 of dissociation between the temporal and spatial dimensions of interlimb coordination, the second experiment explored whether attentional focus could selectively modulate the spatial aspects of the interlimb coordination task without affecting the temporal coupling between the limbs. Experiment 2 showed that when the spatial aspects of the interlimb coordination task were prioritised

not only the movement trajectories but also the temporal variability of the interlimb coordination task were modulated. Interestingly, attentional focus to the spatial dimension of interlimb coordination abolished the inherent performance asymmetries usually observed between the limbs (i.e., spontaneous performance differences between the left-hand and the right-hand and an arm and leg).

Phase 2 of this research explored the neural correlates of dual-task performance involving an interlimb coordination and probe RT task. Single-pulse transcranial magnetic stimulation (TMS) was employed in a series of three experiments to specifically assess the excitability of corticospinal pathways during single- and dual-task performance. The first experiment examined the time course of corticospinal excitability of the tibialis anterior (TA) during the RT interval to a secondary task probe stimulus while simultaneously maintaining bimanual in-phase and anti-phase coordination modes. Although corticospinal excitability of the TA did not differ between the in-phase and anti-phase coordination modes, a large increase in corticospinal excitability was observed between single-task and dual-task performance.

The second experiment examined whether the elevated corticospinal excitability during dual-task performance was a 'motor effect' reflecting increased cortical excitability associated with the performance of the continuous bimanual coordination task or it whether reflected the concurrent performance of two tasks (i.e., a dual-task effect). The results showed that the elevation of corticospinal excitability was due, in part, to the production of bimanual movements. However, a further increase in corticospinal excitability also occurred in the dual-task condition. Thus, the increased corticospinal

excitability appeared to reflect a neural process related to the concurrent performance of two tasks.

A final experiment tested whether the increased corticospinal excitability was a general signature of dual-task performance or specific to interactions within the motor cortex. Dual-task conditions involving either a primary motor task or a primary cognitive task (i.e., tone counting) combined with probe RT were compared. Results showed that increased corticospinal excitability was not a general effect of dual-task performance, but specific to dual-task situations involving motor tasks.

Overall, the findings of the experiments conducted in this research exploring attention and coordination dynamics provided further support to the view that attentional allocation impacts on the coupling strength between the limbs and affects both the temporal and spatial dimensions of interlimb coordination. Furthermore, at the neural level, dual-task effects showed different neural manifestations for structural interference and capacity interference.

## Chapter 1 Introduction

Over the past two decades two different theoretical perspectives, the cognitive or information processing and the dynamical system approach, have dominated the field of human motor control. At the philosophical level, the information processing approach assumes the existence of an internal representation responsible for generating movement patterns. In contrast, the coordination dynamics approach denies such representation arguing that movement patterns emerge in a self-organised manner (for review see Kelso, 1995).

Theoretically, the main assumption of the information processing model for human motor control is founded on the premise that the workings of the brain are analogous to the processing of information by a computer. Central to this model is the concept of a motor program that is viewed as a mechanism that controls motor action. A motor program is defined as *“an abstract representation that, when initiated, results in the production of a coordinated movement sequence”* (Schmidt & Lee, 1999, p. 416). Attention is another important concept developed within this model. For example, whereas some motor actions can be performed without much mental effort or attention, others may require a great deal of attention. According to Schmidt (1999), attention is defined as *“a concept that describes limitations in the processing of information”* (p. 411).

An increasing dissatisfaction with cognitive models, among some researchers, however, resulted in a major paradigmatic crisis in the field precipitated by a view

that motor behaviour is not abstractly represented at a central level – orchestrated by the ‘homunculus’ – but emerges from the interactions of physical and dynamical properties of the motor system (Kelso, Holt, Rubin, & Kugler, 1981; Kugler, Kelso, & Turvey, 1982). The so-called dynamical systems approach seeks, through the application of the concepts and tools of non-linear dynamics and synergetics, to identify principles of biological systems that govern motor action (Kelso, 1995). The theoretical foundation of this approach is based on Bernstein’s view that a coordinated action is a problem of mastering the many degrees of freedom resulting from the environmental, neural, muscular, biomechanical and metabolic components in a particular motion (see Kelso, 1995). For Bernstein (1967), degrees of freedom are not controlled individually but rather are constrained to interact with each other as a single functional unit.

A key feature of this approach is the mathematical model of stability and loss of stability in the formation of movement patterns (for an overview see Summers, 1998). According to Kelso (1995), among all possible states, a dynamical system tends to settle to certain preferred and stable states called attractors (i.e., a fixed point). The main focus of the dynamical systems approach to coordinated movements has been on the phenomenon of phase transitions. That is, the qualitative change of a system’s behaviour from one state to another. Examining the phenomenon of phase transitions in coordinated movements has been useful in the identification of variables that influence the stability of a system as well as in the quantification of the macroscopic variables of coordinated movements.

Despite the pessimistic view of reconciliation between the information processing and coordination dynamics approaches expressed by Abernethy and Sparrow (1992), recently some researchers have attempted to bridge the gap between the two approaches in order to gain a better understanding of motor behaviour (e.g., Monno, Temprado, Zanone, & Laurent, 2002; Summers, Byblow, Bysouth-Young, & Semjen, 1998; Temprado, Zanone, Monno, & Laurent, 1999, 2001). This has been achieved by combining experimental paradigms from both approaches to examine the role of cognition in coordination dynamics. For example, Temprado and colleagues (1999; 2001) using a dual-task paradigm have demonstrated that attention plays a major role in the stabilisation of coordination patterns. In these studies, attention reflecting the allocation of a limited supply of processing resources (Kahneman, 1973) has been linked to the potential function of coordination dynamics.

Recent attempts have also been made to link the observed variables of attention and coordination dynamics to underlying neural activities. Research using functional imaging techniques such as functional resonance magnetic imaging (fMRI), positron emission tomography (PET), superconducting quantum interference device (SQUID), and magnetoencephalography (MEG) have examined neural changes during phase transitions in coordination dynamics (e.g., Fuchs et al., 2000; Mayville et al., 2001), coordination pattern stability (e.g. Jantzen, Fuchs, Mayville, Deecke, & Kelso, 2001), and attentional processes (e.g., Johansen-Berg & Matthews, 2002).

In line with recent trends (Temprado et al., 1999, 2001), this research was concerned with the concurrent performance of two tasks (i.e., dual-task performance),

to further investigate the interaction between attentional processes and coordination dynamics. The present research was divided into two phases. Phase 1 focused on the behavioural aspects and Phase 2 on the neural correlates of dual-task performance. To begin with a review will be presented of two sources of dual-task interference identified within cognitive models, resource and structural interference. Next, the theoretical background of interlimb coordination dynamics and the integration of coordination dynamics and information processing accounts of dual-task performance through the concept of attention will be reviewed. Two experimental studies will then be presented designed to examine the interaction between attention and coordination dynamics, at the behavioural level.

Phase 2 of the thesis will begin with a review of some recent findings associated with the neural correlates of dual-task interference, mainly based on neuro-imaging studies. The transcranial magnetic stimulation (TMS) technique is then outlined and its use in the present research to investigate the neural correlates of dual-task performance described. Finally, some recent findings showing alterations in neurophysiological measures associated with coordination dynamics will be presented. Three experiments are then presented designed to identify the neural correlates of dual-task performance. In these experiments changes in corticospinal excitability are examined during various single- and dual-task conditions.

A final summary presents the main empirical findings and a discussion of the correlates of dual-task structural interference.



## Chapter 2 Literature Review (Part 1)

### 2.1 Attention: A Multidimensional Concept

Despite its ambiguity, the definition offered by Willian James that “*Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others*” (as cited in Schmidt & Lee, 1999, p. 62) still remains the most common citation in the literature when introducing the topic of attention. The difficulty in achieving a universally accepted definition is because attention has been operationalised in different ways. Attention, therefore, is currently characterised as a multidimensional construct with different lines of research focusing on a particular attentional process (Abernethy, Summers, & Ford, 1998).

Attention, for instance, can be seen as a state of alertness or arousal. It has been observed that there is an optimal psychological and/or physiological level of arousal needed to achieve a successful performance (Yerkes & Dodson, 1908). The relationship between the level of arousal and performance has been mapped onto an inverted-U curve. Weinberg and Ragan (1978), for example, have shown that when participants were subjected to low, moderate and high stress conditions during the performance of a motor task (e.g., throw a ball at a target), performance in the moderate stress condition was more successful than in the low and high stress

conditions. Therefore, performance will be affected when arousal is beyond or below this optimal level. The common explanation for the inverted-U curve is that changes in arousal modulate attentional processes (e.g., Moran & Summers, 2004)

Attention has also been linked to the notion of consciousness (Matlin, 1989; Schmidt & Lee, 1999). According to Schneider and Shiffrin (1977), information can be processed in two ways: controlled and automatic. Controlled processing is slow and serial, demanding high levels of attention, and consciousness. In contrast, automatic processing is fast and parallel, therefore non-conscious with low attentional demands. Schneider and Shiffrin demonstrated in a memory search task that when a target letter to be searched in a set of letters was constant (i.e., never changed across trials), responses in RT were similar regardless of the number of letters presented in the set (i.e., one, two or four). These results suggested an automatic process. In contrast, when the target letter to be searched in a set of letters varied across trials, RT increased linearly with the number of letters presented in the set, suggesting a type of controlled processing.

Another aspect of attention is related to the process of selecting relevant information from the environment. To account for the selective component of attention, it was proposed that a filter (i.e., a type of bottleneck) limits the processing of information (Broadbent, 1958; Treisman, 1964). Early experiments involving a dichotic listening paradigm showed that attention was severely limited when divided between two independent channels of auditory verbal input (e.g., Broadbent, 1958). It was hypothesised that the main function of a filter-like mechanism is to prevent an

overload on a single channel system that can only process one chunk of information at a time. Subsequently, bottleneck theory became dichotomised into two distinctive models: early-selection (Broadbent, 1958; Treisman, 1969) and late-selection (Deutsch & Deutsch, 1963; Norman, 1968). According to the early-selection model, information that arrives through sensory channels is maintained for a brief time in what is called sensory memory. Such information is identified and remembered if selected by a filter that passes the information on to a limited capacity processing system. According to Broadbent (1958), the limited capacity channel is equivalent to short-term memory and only events or items that are in a subject's focus of attention reach long-term memory. The late-selection model, in contrast, proposed that the bottleneck does not operate at the sensory level but it comes after long-term memory. Information in this case is processed at the deepest level and the bottleneck is located just prior to the response selection phase.

The other dimension is when attention has to be divided between two concurrent tasks. In this particular, attention is conceptualised as a limited capacity or resource (Kahneman, 1973). According to the author, "*a capacity theory assumes that there is a general limit on man's capacity to perform mental work*" (p. 7). Attention in the resource metaphor is conceived as a 'pool' of undifferentiated mental capacity that can be flexibly allocated according to task demands. A basic assumption underlying Kahneman's limited capacity model is that if the attentional demands of performing two tasks concurrently exceed the total capacity available in the system, then the performance of one or both tasks will degrade.

Attention, therefore, is a construct that has been conceptualised in different forms. The main focus of the present research is the dimension of attention underlying the execution of two tasks simultaneously.

## **2.2 Attention and Dual-Task Methodology**

Dual-task methodology requires the concurrent performance of two tasks, with one of the tasks defined as the primary task and the other as the secondary task. The basic assumption is that the secondary task, usually a discrete probe RT task, provides an assessment of the attentional resources or central cost needed to perform the primary task (Schmidt & Lee, 1999).

For example, Posner and Boies (1971) conducted a study employing probe RT as a secondary task in combination with a primary letter-matching task. In the primary task participants had to depress a key with their right index finger when the same letter was presented in sequence, and another key with their right middle finger when the letters were different. For the auditory probe RT task, participants were required to depress a different key with their left index finger as fast as possible after the presentation of an auditory tone. Thus, probe RT was used to assess the attentional load or central cost of different stages of processing the main task (i.e., letter-matching task). Their results showed that attentional demands (i.e., probe RT) were higher when probe stimuli were delivered after the presentation of the second letter (i.e., in the comparison stage) than when administered after the presentation of the first letter.

Interference is a conspicuous feature of dual-task performance that generally leads to performance decrement of one or both tasks. Two different forms of interference that have been studied within the dual-task paradigm are capacity and structural interference (see Schmidt & Lee, 1999).

### **2.3 Capacity Interference**

Capacity interference stems from several cognitive processes competing for limited processing resources, leading to an observable behaviour known as performance trade-off. That is, the maintenance of performance of one task is accompanied by a measurable cost in the performance of the other task. In general, performance trade-offs occur when more attentional resources are allocated to one of the tasks because of either task difficulty or task priority (Navon & Gopher, 1979). When one of the tasks involves a high level of cognitive processing, then more attentional resources are naturally allocated to that task, thereby leaving fewer attentional resources for the other task. Task priority reflects how efficiently people can allocate their attention by instruction to one or the other task in order to improve the performance of the attended task.

With respect to performance trade-offs, Norman and Bobrow (1975) suggest that a distinction should be made between data-limited and resource-limited tasks. In data-limited tasks, performance is limited by the quality of the information available, such that allocating more attentional resources will not promote further enhancement of performance. In contrast, resource-limited tasks are limited by the amount of

resources devoted to the task, such that task performance increases as more resources are allocated to the task.

Task prioritisation has become an important experimental procedure to examine people's ability to allocate attention in a graded fashion (e.g., Briton & Price, 1981; Tsang, Velazquez, & Vidulich, 1996). Navon (1990) developed the optimum-maximum method to systematically explore the nature of attentional prioritisation in dual-task performance. The method requires participants during attentional prioritisation to strictly maintain the performance of one of the tasks at the best level while maximising the performance of the non-prioritised task, and thus avoids the possibility that performance on the secondary task (i.e., non-prioritised) is sacrificed. The essential aspect of this method is the provision of performance feedback to participants during or after a trial to ensure adherence to the task prioritisation instructions.

Employing the optimum-maximum procedure, Tsang and colleagues (1996) demonstrated a performance trade-off when additional resources were allocated to the primary task (see also Tsang, Shaner, & Vidulich, 1995; Tsang & Wickens, 1988). In this research a continuous tracking task was performed concurrently with the Sternberg memory search task. Attentional prioritisation was manipulated at three different levels: (a) participants were required to produce their best single-task performance in each task; (b) participants were required to divide their attention equally between both tasks and produce their best dual-task performance; (c) participants were required to perform the dual-task according to the optimum-

maximum method. It is worth noting that performance of each task in the dual-task condition where attention was divided equally – even when requiring participants to do their best – tended to be lower than the performance in the single-task conditions. During these dual-task trials, it is important that the experimenter encourages participants to do their best even when this represents an impossible goal (see also Temprado et al., 1999).

In optimum-maximum trials, participants were instructed to prioritise the primary task and attempt to achieve the average performance attained during single-task performance. Participants, however, were encouraged to also maximise the performance of the secondary task. Although Tsang and colleagues (1996) did not provide any explicit performance standard to participants with regard to the performance of the secondary task, the average performance of secondary task during the dual-task with divided attention condition can be used as the performance standard during optimum-maximum trials (see Temprado et al., 1999). Tsang and colleagues (1996) showed that when the tracking task was prioritised the performance of the memory search task (i.e., the secondary task) decreased significantly compared with the dual-task situation in which attention was divided between the tasks. According to the authors, the performance trade-off observed cannot be interpreted as an experimental artefact but rather as indicative of the voluntary control of the allocation of limited attentional resources.

## 2.4 Structural interference

Limitations in the form of structural interference occur when two tasks involve similar physical or neurological structures (Navon, 1985; Navon & Miller, 1987). The main focus of the structural interference account relates to the extent to which structures of the CNS involved in the dual-task performance interfere with each other. According to Navon and Miller (1987), structure interference between two tasks may not only be due to competition between similar inputs or neural mechanisms “*but also because each produces outputs, throughputs, or side effects that are harmful to the processing of the other one*” (, p. 435). This effect has been termed outcome conflict. Expressions of structural interference from one task to another, presumably occurring at any level of the CNS, are often reported in human behaviour in the form of halting (e.g., de Hoon et al., 2003), phase wandering (Summers et al., 1998) or changes in kinematics (O’Shea, Morris, & Ianse, 2002; Vuillerme, Nougier, & Teasdale, 2000).

Signs of structural interference are observed when responses for the concurrent tasks share similar output mechanisms. McLeod (1980), for example, demonstrated that RT to a probe task requiring manual response with the left hand combined with an aimed discrete movement performed with the right hand was significantly longer than when the probe task required a vocal response. This study clearly indicates that the response modality of the probe RT task is an important factor in determining the degree of interference in dual-task performance. It was



argued that the difficulty in the performing manual-manual response combination was due to difficulty in selecting and executing two independent motor responses.

In a related study, McLeod (1977) reported that the difficulty of performing a manual-manual response combination also affected the performance of the primary continuous tracking task compared with manual-vocal response combination. That is, movement trajectories of the tracking task were more accurate during vocal probe RT than manual probe RT. The latter condition appeared to produce greater structural interference than vocal probe RT. It was concluded that the vocal probe RT as a secondary task provided a more pure measure of central capacity than motor probe RT.

Structural interference has been linked to the functional cerebral distance between concurrent activities (Kinsbourne & Hicks, 1978). The smaller the functional distance between cerebral regions with respect to the cerebral structures involved in the dual-task the greater the interference in the performance on one or both tasks. For example, it has been shown that speech interferes more with actions such as dowel balancing (Kinsbourne & Cook, 1971) and finger tapping (Bathurst & Kee, 1994; Hiscock & Chipuer, 1986) executed with the right-hand than with the left-hand. It was hypothesised that the strong interference observed was a consequence of the cerebral functions associated with both right manual action and speech being located in the same (left) hemisphere.

Recent theorising suggests that the two interpretations of dual-task limitations, capacity and structural interference, are not mutually exclusive but may co-exist and

that a better understanding of attentional factors may be gained by bridging the gap between the two interpretations (Temprado et al., 2001). A theoretical framework that blends the two interpretations of dual-task limitations will be discussed later.

## **2.5 Dynamics of Interlimb Coordination**

The aim of the present research is to examine further the link between attentional process from a cognitive perspective and coordination dynamics. From the perspective of coordination dynamics, it is essential to understand how the elements of a biokinematic system can be assembled temporarily to achieve a particular task goal and how the stability of movement coordination emerging from a variety of constraints can be maintained without losing flexibility. An important contribution to the understanding of behavioural flexibility has come from the dynamical systems approach. Central features of this approach are that inherent or spontaneous coordination tendencies influence the emergence of new stable coordination patterns, and that coordination patterns emerge from the reciprocal influence of various components of a system (e.g., neural, muscular, metabolic).

Support for dynamical accounts has come from studies of bimanual coordination that have identified two elementary coordination modes, in-phase and anti-phase (Kelso, 1984, 1995). Typically, the in-phase coordination mode involves symmetrical movements of the hands or fingers with simultaneous activation of homologous muscles, whereas the anti-phase coordination mode involves asymmetrical motions of the limbs with simultaneous activation of non-homologous

muscles. Relative phase between the limbs or segments and relative phase variability constitute collective variables that capture the organisational state of the system. Whereas relative phase refers to the spatio-temporal advancement of one limb with respect to the other in an oscillation cycle, relative phase variability reflects the system's stability. Studies have repeatedly demonstrated that the in-phase coordination mode is more stable than the anti-phase mode, and importantly, an involuntary and abrupt phase transition from initial anti-phase coordination to in-phase occurs when the frequency of oscillation reaches a critical value (e.g., Kelso, 1984; Kelso, Scholz, & Schöner, 1986). Phase transitions result from the loss of stability of a pattern – which is assessed by means of the variability of the phase differences between the limbs – and are preceded by critical fluctuations of relative phase (Kelso et al., 1986).

Such spontaneous coordination dynamics have been modelled in the form of a potential function (the so-called HKB model) that represents an equation of motion of a collective variable (i.e., relative phase), which captures the relation between the moving components (Haken, Kelso, & Bunz, 1985). A very accessible way to understand the HKB model (Figure 1) is by looking at the representation of the system's current coordination state as a landscape of valleys. The deeper the valleys, the more stable the system. The equation of the HKB model ( $V = -a \cos \phi - b \cos 2\phi$ ) describes the potential function of two cosine functions, where  $a$  and  $b$  are constant parameters dependent on a control parameter, in this case, oscillation frequency. Then, in given ratios between the parameters  $a$  and  $b$ , specifically those related to

comfortable oscillation frequencies, two relatively deep and stable valleys can be seen representing in-phase and anti-phase coordination modes. However, increasing the oscillation frequency changes the ratio between  $a$  and  $b$  and the valleys become shallower, thus reducing system stability. An important aspect of the in-phase coordination mode is that although the valley has become shallow, it is still sufficiently deep to maintain a fairly stable system. That is not the case for the anti-phase coordination mode. In summary, the relative depths of the two valleys may vary as a function of the ratio between  $a$  and  $b$  which is determined by the frequency of oscillation. It is through changes to the ratio that the stability of a specific coordination pattern is modified.

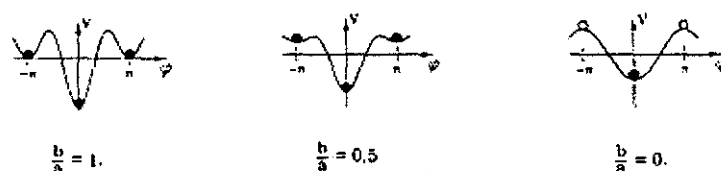


Figure 1. The little ball illustrates the behavior of the system initially prepared (upper left corner) in the anti-phase. White balls are unstable states; black balls are stable (adapted from Kelso, 1995).

The initial work modelling bimanual coordination as a nonlinear limit cycle oscillatory system had used an index finger oscillation task, involving simple one-dimensional movements. A question of interest for other researchers was whether similar coordination dynamics would be exhibited in multi-joint bimanual coordination. An exemplar experimental task is bimanual circle drawing (Semjen, Summers, & Cattaert, 1995). This task involves tracing continuously the contours of two circles with the index fingers in either an in-phase or symmetrical mode (e.g., one

hand moving clockwise, the other counter-clockwise) or an anti-phase or asymmetrical mode (i.e., both hands moving clockwise or counter clockwise). A particular feature of the circle drawing task is that it involves coordination in both temporal and spatial dimensions, requiring precise phasing of the hands and accurate production of circular trajectories with each hand, respectively. Across a number of studies the dynamics of the bimanual circle-drawing task, which involves shoulder, elbow and wrist joints, have been shown to share many similarities to the coordination dynamics of single-joint tasks (e.g., Carson, Thomas, Summers, Walters, & Semjen, 1997; Semjen et al., 1995; Summers, Semjen, Carson, & Thomas, 1995; Swinnen, Jardin, Meulenbroek, Dounskaia, & HofkensVanDenBrandt, 1997; Wuyts, Summers, Carson, Byblow, & Semjen, 1996).

Consistent findings obtained in studies using the circle drawing task are: (a) the symmetric coordination mode is more stable than the asymmetric coordination mode; (b) the asymmetric coordination mode becomes unstable at high movement rates and can exhibit a spontaneous transition to the symmetric coordination mode; (c) these coordination dynamics are consistent for both right-handers and left-handers and across proximal and distal muscle groups. Manual asymmetries are also evident in the circling task and are of a greater magnitude than the asymmetries usually observed in single joint task dynamics. Specifically, with increasing movement frequency the non-dominant hand exhibits severe trajectory distortions and/or increasingly lags behind the dominant hand resulting in de-phasing of the hands. Furthermore, when a spontaneous transition occurs it is almost exclusively the non-

dominant hand that makes the transition through a reversal in direction (e.g., Byblow, Chua, Bysouth-Young, & Summers, 1999; Semjen et al., 1995).

The constraints on behaviour imposed by the underlying coordination dynamics do not preclude flexibility. Such flexibility is achieved through an additional attractive force, called behavioural information, that influences behaviour by competing or cooperating with the spontaneous dynamics of coordination patterns (Schöner & Kelso, 1988). It is through the concept of behavioural information that factors such as perception, memory, attention, volition or learning can influence the coordination dynamics. For example, subjects can intentionally delay or resist the phase transition from anti-phase coordination to in-phase as frequency increases (Lee, Blandin, & Proteau, 1996), stabilise a new coordination pattern with learning (Schöner, Zanone, & Kelso, 1992; Zanone & Kelso, 1992), or enhance spatial and temporal performance of the non-dominant hand by directing visual attention to it (Wuyts et al., 1996). Central to these studies has been the assumption that the supplementary attractive force exerts its influence by changing the information coupling among the components of a coordinated system, thereby altering the dynamics of intrinsic patterns. This interaction between coordination dynamics and behavioural information can be seen as cognitive processes overriding intrinsic dynamics (Semjen et al., 1995; Summers, 1998).

## 2.6 Coordination Dynamics and Attention

Coordination dynamics capture how the nervous system stabilises and destabilises coordinated behaviour. The dynamics of the potential function has been linked to the amount of energy, specifically the metabolic energy, necessary for the system to maintain coordination patterns in a given state (Diedrich & Warren, 1995; Hoyt & Taylor, 1981). For example, preferred patterns of gait in both humans and horses are associated with minimal levels of metabolic and mechanical energy consumption. Accordingly, the most stable patterns are energetically the least expensive, whereas coordination patterns away from the preferred states require additional energy expenditure. Recently, it has been proposed that not only metabolic or mechanical energy but also a type of ‘mental energy’ is entailed in the production of coordinated patterns (e.g., Temprado et al., 1999). Specifically, it has been proposed that the information processing concept of attentional load can be used as a measure of mental energy or effort, as it is seen to approximately reflect the intensity of CNS processing activity required to maintain and stabilise a coordination pattern against inherent perturbing stochastic forces. Operationally, the link between attention and coordination dynamics has been examined within a dual-task paradigm involving the concurrent performance of a continuous bimanual coordination task and a discrete secondary task (see Monno et al., 2002 for a review). The blending between dual-task and coordination dynamic paradigms has not only shown that concepts developed

within cognitive psychology and coordination dynamics are not completely incompatible but also demonstrated the role of attention in interlimb coordination.

The central cost of stabilising bimanual coordination patterns has been examined by Temprado and colleagues (1999; 2001). In these studies, a dual-task paradigm was employed involving the concurrent performance of rhythmic forearm supination and pronation movements and a discrete auditory probe RT task. Attention direction was manipulated by instructing participants to divide attention equally between both tasks or to prioritise one of the tasks employing the optimum-maximum method (Tsang et al., 1996). Two important results have been obtained. First, directing attention to the coordination task enhanced coordination stability, but increased RT to secondary task probes, producing a classical performance trade-off. Furthermore, the differential inherent stability between in-phase and anti-phase coordination modes was not abolished by attentional prioritisation. Second, bimanual pattern stability and attention demands were found to strongly co-vary: the more stable a pattern the less the attentional/central cost associated with maintaining that pattern. In sum, Temprado and colleagues (1999) showed that maintenance of the in-phase and anti-phase coordination modes was systematically associated with different attentional costs, such that the anti-phase coordination incurs a higher central cost than the in-phase mode.

Temprado and colleagues (2001) argue that the allocation of attentional resources increases the coupling strength between the limbs. As coupling strength increases, the coordination becomes more resistant to perturbations (i.e., structural



interference) from a secondary task. Support for this hypothesis has come from moment-by-moment analysis (i.e., examining changes in interlimb coordination performance half cycle by half cycle around the probe response). This analysis has shown that attentional prioritisation of the bimanual coordination task reduced the effects of responding to secondary task probes on primary task performance compared to when attention was divided between the two tasks. In agreement with predictions from coordination dynamics, Temprado and colleagues (1999) found that the anti-phase coordination mode, but not the in-phase mode, was affected by probe RT. However, attentional prioritisation was capable of reducing the structural interference effect caused by the probe response. Thus, the central nervous system (CNS) through resource allocation determines the degree of structural interference by varying the coupling strength between the limbs.

Summers, Byblow, Bysouth-Young, and Semjen (1998) also found that the differential stability observed between in-phase and anti-phase coordination modes in a bimanual circle drawing task, when performed at a fast rate, was reflected in performance on a concurrent tone counting task. It was suggested that the greater attentional effort required to maintain anti-phase movements, especially at high movement rates, was a consequence of the necessity to consciously monitor kinesthetic information to prevent a spontaneous switch to in-phase coordination. Other studies have shown that directing attention to one limb during performance of a bimanual circle-drawing task modulated both the temporal and spatial aspects of the task (Swinnen, Jardin, & Meulenbroek, 1996; Wuyts et al., 1996). For example,

visual attention to the non-dominant hand enhanced movement circularity in that limb, whereas directing attention to the dominant limb did not improve movement circularity (Wuyts et al., 1996). In addition, Swinnen and colleagues (1996) showed that visual attention to the left- or right-hand modulated the size of asynchrony between the hands. Specifically, relative phase offset increased when vision was directed towards the dominant hand, and decreased when visual attention was directed to the non-dominant hand compared to free visual attention and blindfolded conditions.

## **2.7 Constraints on Interlimb Coordination**

It has recently been shown that not only do supplementary forces such as attention and intention impact upon coordination stability and its cognitive load but constraints on coordination, such as egocentric (i.e., simultaneous movements towards and away from the body midline), directional or allocentric (i.e., simultaneous movements in the same direction), and muscular (i.e., simultaneous homologous muscular activation) also either facilitate or reduce coordination stability (Park, Collins, & Turvey, 2001; Temprado, Swinnen, Carson, Tourment, & Laurent, 2003). For example, Temprado and colleagues (2003) demonstrated that for between-persons coordination same direction movements (i.e., anti-phase mode) improved stability, whereas for within-person coordination muscle homology, in particular in-phase movements with an egocentric frame of reference, was a greater determinant of stability than direction of the moving limbs. When movements were performed in the

sagittal plane in order to eliminate the confounding influence of the egocentric constraint, both the isodirectionality and the muscle homology principles appeared to exert independent influences on coordination. The demonstration of a muscle homology effect in the absence of the egocentric constraint does not support the extreme view recently expressed by Mechsner and colleagues (2001) that all motor symmetry effects are purely perceptual. Furthermore, Temprado and colleagues (2003) showed that bimanual pronation-supination movements performed non-isodirectionally (i.e., different directions) in the frontal plane activating non-homologous muscles not only had a destabilising effect on coordination but also were associated with an increase in an attentional load measure (i.e., high probe RT). On the other hand, non-isodirectionality combined with muscular homology in the lateral plane of motion (mirror movements) contributed to stabilising the coordinated pattern as well as reducing attentional demand (i.e., shorter probe RTs).

## **2.8 Probe RT Response Type**

The type of response made to probe task stimuli during dual-task performance can also influence the performance of a primary task. Temprado and colleagues (1999; 2001) employed a moment-by-moment analysis consisting of analysing interlimb coordination performance half cycle by half cycle around the probe stimulus (see also Tsang et al., 1995; Tsang et al., 1996). Of interest was whether primary task performance (i.e., relative phase and its stability) was perturbed by responses to probe stimuli indicating the presence of structural interference. The results showed that

relative phase accuracy was lowered for a half cycle following responses to probe stimuli but recovered by the next half cycle, irrespective of whether responses to probe stimuli were made with the feet (Temprado et al., 2001) or fingers (Temprado et al., 1999). It has been argued, however, that vocal probe RT task provides a better measure of central resource allocation (McLeod, 1977).

A study conducted by Elder (2001a) comparing probe RT responses performed with either the foot or voice during a bimanual circle drawing task showed that coordination task performance was less stable in terms of both the coupling between the limbs, and the circularity and variability of the movement trajectories produced by each hand, when responses to probe stimuli were made with the foot. These results support the view that vocal responses may represent a more pure index of costs at the central level. In addition, a moment-by-moment analysis – a cycle by cycle analysis around probe stimulus delivery showed that coordination stability decreased in the first cycle after probe stimulus delivery when foot responses were made but not for vocal responses (Elder, 2001b).

## **2.9 Summary**

Previous research has demonstrated that coordination of the upper limbs, especially in the anti-phase mode, demands attentional resources. Furthermore, the allocation of attention has been shown to be a variable capable of strengthening the coupling between homologous pairs of limbs (e.g., upper limbs) and enhancing coordination stability. Two questions concerning the interaction between attention and

coordination dynamics, at the behavioural level, are of interest in the present research:

(a) whether the strong co-variance between pattern stability and attention observed between homologous pairs of limbs would be evident in the coordination of non-homologous limb combinations (i.e., an arm and leg), as there is some evidence that the coordination dynamics differ; (b) whether attention focus would constitute a parameter capable of dissociating spatial and temporal characteristics in a multijoint interlimb coordination task (e.g., circle-drawing).

## **Chapter 3 Experimental Study 1**

### **3.1 Coordination Across Limbs: Upper limbs, Contralateral And Ipsilateral Limb Combinations**

Two types of non-homologous limb coordination (i.e., coordination involving arm and leg) have been frequently studied, contralateral and ipsilateral limb combinations. Contralateral coordination involves the simultaneous motions of diagonal limb pairs (e.g., left arm and right leg), whereas ipsilateral coordination involves limbs on the same side of the body (e.g., right arm and right leg). It is well established from studies involving continuous flexion-extension movements of the upper or lower limbs in the sagittal plane (i.e., homologous limb combinations) move in a more synchronised and stable fashion than non-homologous limb combinations (Kelso & Jeka, 1992; Serrien & Swinnen, 1997a, 1997b, 1998a, 1998b; Swinnen, Dounskaia, Verschueren, Serrien, & Daelman, 1995). Similar results have been found with a circle drawing task (Swinnen et al., 1997). The difference in stability between homologous and non-homologous limb combinations may reflect the strength of the motor-neuronal circuitry between the segments (Serrien & Swinnen, 1998b; Swinnen, 2002). In this respect, one might expect that the coordination of non-homologous limb combinations would be associated with higher central costs than the coordination of homologous limb combinations.

Furthermore, moving non-homologous limb combinations in the same direction (i.e., iso-directional) in external space (i.e., movement direction of one limb

with respect to the other) results in more synchronised and stable coordination than moving the limbs in different directions (i.e., non-isodirectional), with a stronger effect evident for ipsilateral than contralateral limb combinations (Baldissera, Cavallari, & Civaschi, 1982; Baldissera, Cavallari, Marini, & Tassone, 1991; Serrien, Li, Steyvers, Debaere, & Swinnen, 2001; Serrien & Swinnen, 1997a, 1997b; Swinnen et al., 1997). To be consistent with the terminology used in most previous studies of non-homologous limb coordination and to allow comparison with the homologous limb coordination, movements of contralateral or ipsilateral limbs in the same direction will be referred to as in-phase coordination and movements in opposite directions as anti-phase coordination.

Interlimb coordination stability, however, depends not only on neuromuscular coupling between the limbs but also on the interaction between a variety of constraints operating upon a coordination system which may stabilise or destabilise a coordination pattern (Carson & Kelso, 2004). In particular, muscular constraints expressed by a preference for activating simultaneously homologous muscles (Kelso, 1984; Scholz & Kelso, 1989), and the egocentric constraint denoted as a preference for simultaneously moving limb pairs toward and away from the body midline<sup>1</sup> (Swinnen et al., 1997; Temprado et al., 2003) have been shown to play a major role in determining the stability of homologous limb combinations (i.e., both arms or both legs). A further form of constraint referred to as allocentric, that is preference for

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<sup>1</sup> In previous studies of bimanual coordination the egocentric constraint has been linked to simultaneous activation of homologous muscle (e.g., Swinnen et al. 1997; Swinnen, 2002). Here the term egocentric is used to refer to direction of movement with respect to the longitudinal axis of the body without reference to homologous muscle activation.

moving limbs in the same direction with respect to external space (i.e., movement direction of one limb with respect to the other), has also been shown to exert a strong influence, particularly on coordination of non-homologous limbs. Moving upper and lower limbs in the same direction (i.e., isodirectional) results in a more synchronised and stable coordination than moving the limbs in different directions (i.e., non-isodirectional), with a stronger effect evident in ipsilateral than contralateral limb combinations (Baldissera et al., 1982; Baldissera et al., 1991; Serrien et al., 2001; Serrien & Swinnen, 1997a, 1997b; Swinnen et al., 1997).

### **3.2 Aims of the study and predictions**

Two main issues were examined in the present study. The first related to whether the effects of attentional prioritisation on the stability of a coordination pattern observed for single-joint bimanual movements (i.e., pronation-supination of the forearms) would be evident in the coordination of upper and lower limbs in multisegmental movements. According to the dynamical systems approach, intentional stabilisation via attentional focus is viewed as an additional force that may alter stability of coordination patterns by changing the coupling strength between the limbs. The second issue was whether a relationship between stability and central cost would be observed across both homologous (i.e., upper limbs) and non-homologous (i.e., contralateral and ipsilateral) limb combinations. Since attentional cost represents the amount of activity required by the CNS to maintain the coupling between components



(Monno et al., 2002), then coordinating non-homologous limb combinations should demand more attentional resources than coordinating homologous limb combinations.

### **3.3 Method**

#### **3.3.1 Participants**

Eighteen volunteers (4 men, 14 women), aged 19 - 54 years (mean = 31 years), from the University of Tasmania participated in the experiment. All participants selected were right-handed and right-footed based on answers from an adapted Oldfield (1971) questionnaire (see Appendix 1). Written informed consent was obtained prior to participation in the study. Ethics approval for the study was obtained from the University of Tasmania Human Research Ethics Committee.

#### **3.3.2 Apparatus**

Participants were seated comfortably in a height adjustable chair. A platform was set on the floor, and a circle template (10 cm diameter) was positioned on its surface for circling with the right foot. Two adjustable platforms were positioned in front with one slightly to the right and the other to the left side of the participant's midline for circling with the upper limbs. A circle template (10 cm diameter) was positioned on each platform's surface. An OPTOTRAK 3020 active infrared motion analysis system, sampling at 200 Hz, was used to track the movement of infrared light-emitting diodes (IREDs) placed on the fingertips of the participant's index fingers or on the first toe of the right foot.

### 3.3.3 Procedure

Participants were asked to trace continuously the contour of the circle templates with both index fingertips or with their fingertip and toe, depending on the condition.

Three limb combinations were performed in the in-phase and anti-phase coordination mode: (1) upper limbs, (2) contralateral – left arm/right leg, (3) ipsilateral – right arm/right leg (Figure 2). As previously mentioned, the in-phase and anti-phase coordination modes were defined to be consistent with previous research on interlimb coordination (Swinnen et al., 1997), with the stable pattern defined as in-phase and less stable pattern as anti-phase. Thus, for the homologous limb combination (i.e., both upper limbs) the in-phase pattern involved the left-arm circling anti-clockwise and the right-arm clockwise (i.e., muscular coupling), whereas the anti-phase pattern consisted of both arms circling anti-clockwise (i.e., non-muscular coupling). For the contralateral and ipsilateral limb combinations, the in-phase pattern required both limbs moving anti-clockwise (i.e., iso-directional), whereas in the anti-phase pattern the arm circled anti-clockwise and the leg clockwise (i.e., non-isodirectional). The right leg was supported by a sling to compensate for isometric muscle contraction of the hip flexors when elevating the leg during the task from a seated position. The sling was attached to a long metal bar mounted transversally over two solid stands placed on the left and right side of participant's chair. The three limb combination pairs and two coordination patterns resulted in six different limb combinations. Participants were tested over three experimental sessions with a different limb

combination condition being performed under both coordination modes each session.

The order of limb combination over sessions was counterbalanced across participants.

Each session lasted about two hours and consisted of three parts:


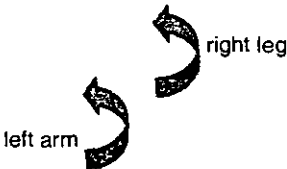
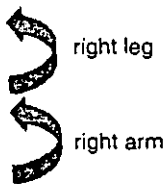
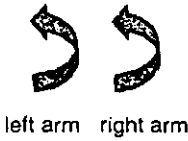
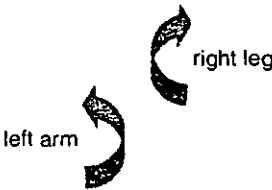
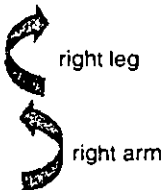
	Homologous	Contralateral	Ipsilateral
In-phase	 left arm    right arm	 left arm    right leg	 right leg right arm
Anti-phase	 left arm    right arm	 left arm    right leg	 right leg right arm

Figure 2. Schematic overview of experimental conditions. Arrows indicate movement direction during interlimb circle-drawing task.

*Part 1: Single tasks* – Three single-task conditions were tested at the beginning of each session: (a) the coordination task in in-phase and (b) anti-phase; and (c) the probe reaction time task – which was only performed in the first session. Each trial for the three tasks was 20 seconds duration. Participants were given at least five practice trials for each of the tasks to familiarise them with the target oscillation frequency of 1 Hz. At the end of each practice trial, feedback was given regarding the extent to which they had deviated from the required frequency.

Participants then performed six trials of the coordination task in each coordination mode. Instructions emphasised maintaining the temporal

synchronisation between the limbs throughout the 20 seconds trial. Only the last four trials were computed for further analyses. At the end of each trial, feedback regarding the temporal aspects of performance (i.e., relative phase and its consistency) was given to participants as an incentive to improve their performance on the next attempt. Mean movement frequency was also reported to ensure that they maintained the required 1 Hz frequency across trials. The order of coordination mode was counterbalanced across participants.

For the probe RT task, participants were asked to voice the word “tone” as quickly as possible after the onset of a tone. A vocal response was chosen to reduce the possibility of structural interference that might occur using the same output responses for the two tasks (Tsang et al., 1995). Tones consisted of 1400 Hz computer-generated signals of 50 ms length presented via loudspeakers. Responses were recorded through a microphone attached to headphones set around the participant’s head. The microphone was placed in front and 3 cm away from participant’s mouth. Six to eight tones were administered randomly per trial. The inter-tone interval was between 600 to 4000 milliseconds. Eight trials of the baseline RT task were performed with explicit attention on the RT task, in which participants reacted to the tone onset as quickly as possible. However, only the last six trials were computed for further analyses. After each trial, the average RT for that trial was given to participants with instructions to attempt to improve on the next trial. The order of interlimb coordination and reaction time tasks was counterbalanced across participants.

*Part 2: Dual tasks* – After completion of single task conditions, dual-task trials (interlimb coordination + RT) were performed under two different attentional priority conditions: (a) attention equally divided between the interlimb coordination task and RT task; and (b) attentional priority given to the interlimb coordination task. For each dual-task condition, six trials were administered for each limb combination condition in both in-phase and anti-phase coordination modes. Only the last four trials in each condition were used for further analyses. The order of coordination modes was counterbalanced across participants.

In the dual-task conditions, the optimum-maximum method was employed (Navon, 1990; see also Temprado et al., 1999; Tsang et al., 1996). In the dual-task with divided attention condition, participants were requested to produce the level of performance obtained in the single tasks. That is, the experimenter encouraged participants to maintain an optimum performance on both tasks even though it represented an impossible goal, but was used to ensure that they did not reduce the attentional effort devoted to either task. In the dual-task with attentional priority condition, participants were asked to produce an optimum performance in the coordination task similar to that obtained in the single-task condition, whereas for the non-priority reaction time task, the performance to be achieved was that of the divided attention condition. After each trial, the circling frequency, relative phase, relative phase variability (i.e., uniformity) and RT values obtained were shown to participants as an incentive to improve their performance on the next trial.

### 3.3.4 Data reduction and dependent measures

Data were low-pass filtered using a second-order Butterworth dual-pass filter with a cut-off frequency of 5 Hz. Continuous tangential angles for each limb were then derived from the normalised displacement time series and applying the two-point central difference algorithm. The magnitude of each vector corresponded to the instantaneous tangential velocity, and the angle of the vector was the tangential angle. RTA (Relative Tangential Angle), a measure of temporal relationship of two components (both arms or an arm and leg) was determined by subtracting the angle of one limb from the other. This measure provides in degrees, the lead-lag time of one limb in relation to the other in their respective movement cycles, with a value of 0 indicating perfect synchronisation between the limbs. Absolute error of RTA (AE of RTA) was used as a measure of performance accuracy. AE of RTA is a non-signed relative phase and was calculated by subtracting the obtained RTA of each trial from the phase relationship target. Uniformity, the dispersion of the relative tangential angle, was calculated as a measure of RTA variability (Mardia, 1972). Small dispersion of the RTA gives a uniformity value close to 1 (i.e., less variable), while the maximum dispersion is indicated by a uniformity value of 0 (i.e., more variable). A suitable transformation of the circular variance to the range 0- $\infty$ , permitting the use of inferential statistics based on standard normal theory, is expressed in the following form:

$$s_0 = [-2 \log_e(1 - S_0)]^{0.5}$$

where  $S_0$  is the measure of uniformity in the range 0-1, and  $s_0$  is the transformed uniformity measure (see also Byblow, Summers, & Thomas, 2000). Untransformed measures of uniformity are reported in the text for clarity.

In the spatial dimension of the circle-drawing task, aspect ratio, a measure of the circularity of movement trajectories produced by each hand was calculated following the procedure described by Walters and Carson (1997). An index of circularity was derived from the ratio of the lengths of the major and minor axes of the best fitting ellipse for each movement cycle. An aspect ratio of 1 indicates a perfect circle and an aspect ratio of 0 indicates a straight line. Aspect ratio values were subjected to arc sine transformation prior to statistical analysis. Untransformed values of aspect ratio are reported in the text for clarity. A measure of variability of movement circularity, spatial error, was derived from the dispersion of circle trajectories of each limb. This was done by calculating the absolute error of the perpendicular distances between the individual data points and the best fitting ellipse (Walters and Carson, 1997).

A custom peak-picking algorithm was used to estimate movement frequency. Deviation of movement frequency was used as a measure of the accuracy with which participants were able to maintain the required movement.

Probe reaction time was defined as the delay between the acoustic signal and the onset of voicing the word “tone”. For subsequent analysis of RT data, probe RTs of the single task (36 to 48 per participant) were randomly distributed into six roughly

equal groups and assigned as single-task baselines for the six dual-task conditions. The six single-task baseline means did not differ significantly ( $p > 0.05$ ).

Repeated measures ANOVAs were utilised for each dependent variable. In addition, Huynh-Feldt epsilon corrections were applied, where appropriate, to the degrees of freedom for  $F$  tests to compensate for violation of homogeneity assumptions. Significant main effects were analysed using Tukey post hoc tests. Interactions between factors were analysed through the simple effects and contrasts by  $t$ -tests. A conventional alpha level of 0.05 was adopted to indicate statistical differences between means.

### 3.4 Results

To examine the effects of attentional prioritisation on the coordination of different limb combinations, each dependent variable was submitted to a 3 X 3 X 2 (Limb Combination X Attention Condition X Coordination Mode) ANOVA with repeated measures on all factors, unless stated differently. The three levels of limb combination were upper limbs, contralateral (left-arm and right leg) and ipsilateral (right-arm and right-leg). Attention consisted of three levels: single-task, dual-task with divided attention, and dual-task with priority on the motor task. The two levels of coordination mode were in-phase and anti-phase. Data pertaining to both limbs in each limb combination were combined for statistical analysis of aspect ratio and spatial error. Additional analyses were conducted for aspect ratio and spatial error to examine differences between the limbs for each limb combination.



### 3.4.1 Conformity to movement frequency oscillation

*Movement frequency deviation.* The mean movement frequency deviation across experimental conditions for all participants was 0.01 Hz (range -0.25 to 0.20 Hz), indicating that participants were able to maintain the required movement frequency (1 Hz).

### 3.4.2 Effects of attentional prioritisation on the coordination task

*AE of RTA.* Statistical analysis revealed significant main effects of limb combination,  $F(1.6, 27.7) = 9.36, p < 0.001$ , coordination mode,  $F(1, 17) = 24.50, p < 0.001$ , and attention,  $F(1.8, 30.6) = 4.41, p < 0.05$ . The following two-way interactions were also significant: limb combination x coordination mode,  $F(2, 34) = 5.59, p < 0.01$ , and attention x coordination mode,  $F(2, 34) = 3.52, p < 0.05$ .

Further examination of the limb combination by coordination mode interaction (see Figure 3) showed that for in-phase coordination the upper limb combination ( $5.64^\circ$ ) was significantly more accurate than both the contralateral ( $10.88^\circ$ ), and ipsilateral ( $12.53^\circ$ ) limb combinations (all  $p < 0.05$ ). During the anti-phase coordination, mean absolute error of RTA for upper ( $11.41^\circ$ ) and contralateral ( $14.25^\circ$ ) limb pairs did not differ but both evidenced smaller error than the ipsilateral limb combination ( $26.79^\circ$ , all  $p < 0.01$ ). As expected, error in RTA was significantly greater under the anti-phase than the in-phase coordination mode in both upper and ipsilateral limb combinations,  $t(17) = -2.85, p < 0.01$ , and  $t(17) = -4.18, p < 0.001$ ,

respectively. Interestingly, no difference was observed between coordination modes in the contralateral limb combination.

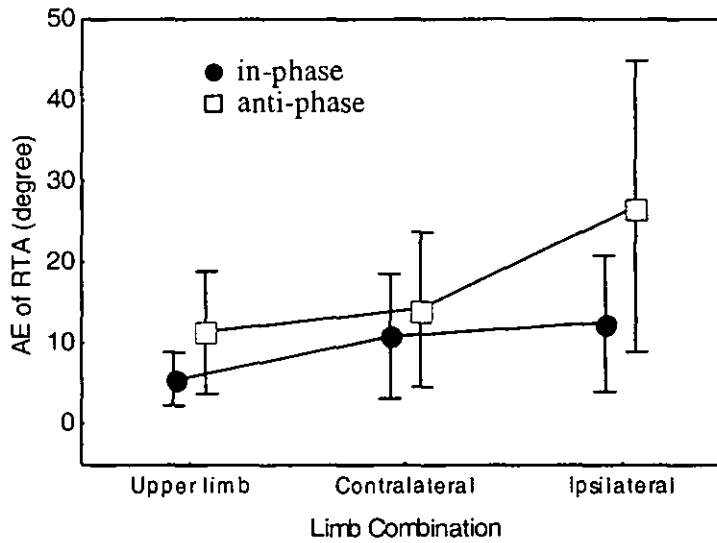


Figure 3. Mean AE of RTA for in-phase and anti-phase coordination modes as a function of limb combination conditions. Error bars represent 95% confidence intervals.

The significant attention by coordination mode interaction (see Figure 4A) indicated that while attention direction did not affect movements during in-phase coordination, it influenced movements prepared in the anti-phase coordination. Specifically, error in RTA under the dual-task with divided attention condition ( $19.48^\circ$ ) was significantly greater than the two remaining conditions (single-task =  $16.21^\circ$ ; dual-task with priority =  $16.76^\circ$ , all  $p < 0.01$ ).

*Uniformity of RTA.* There were significant main effects of limb combination,  $F(1.8, 30.9) = 188.60$ ,  $p < 0.001$ , attention,  $F(2, 34) = 15.06$ ,  $p < 0.001$ , and coordination mode,  $F(1, 17) = 151.99$ ,  $p < 0.001$ . Post hoc tests for the main effect of

attention (see Figure 4B) revealed that performance in the single-task (0.965) and dual-task with attention priority on coordination (0.962) conditions did not differ but both conditions were less variable (i.e., higher uniformity) than the dual-task with divided attention condition (0.957), all  $p < 0.01$ .

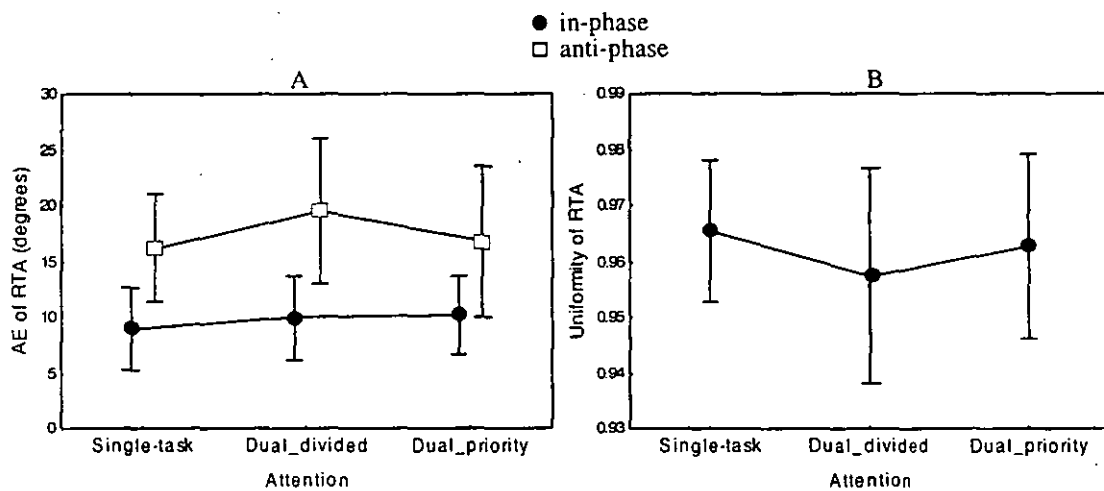


Figure 4. (A) Mean AE of RTA for in-phase and anti-phase coordination modes as a function of attention conditions. (B) Mean uniformity of RTA for single-task, dual-task with divided attention, dual-task with attentional priority on coordination. Error bars represent 95% confidence intervals.

The only significant interaction was limb combination x coordination mode,  $F(1.7, 29.2) = 39.51$ ,  $p < 0.001$ , which qualifies the significant main effects reported above. Further examination of the interaction (see Figure 5A) showed that during in-phase coordination the upper limb combination (0.991) was significantly more stable than both the contralateral (0.954) and ipsilateral (0.960) limb combinations (all  $p < 0.001$ ), which did not differ significantly. For the anti-phase coordination, significant differences in stability were observed among all limb combination pairs (upper = 0.981; contralateral = 0.956; ipsilateral = 0.925, all  $p < 0.001$ ). Comparisons between

the coordination modes for each limb combination condition showed that in-phase coordination was significantly more stable than anti-phase coordination for the upper,  $t(17) = 12.16, p < 0.001$ , and ipsilateral,  $t(17) = 8.17, p < 0.001$ , but not for the contralateral limb combination.

In sum, the effects on mean AE of RTA and uniformity of RTA showed that whereas attentional prioritisation on the coordination task during dual-task performance improved performance both in terms of AE of RTA and coordination stability (i.e., uniformity of RTA), dividing attention equally between the two tasks decreased RTA accuracy as well as coordination stability. Also, of importance are the results showing a decrement in performance for both coordination modes across limb combinations, with greater performance differences apparent in the anti-phase mode, particularly during the ipsilateral limb combination.

### 3.4.3 Attentional load associated with interlimb coordination

*Probe reaction time.* A 3 X 3 X 2 (Limb Combination X Attention X Coordination Mode) ANOVA with repeated measures on all factors carried out on the mean RT yielded a significant main effect of attention,  $F(1.4, 25.3) = 78.59, p < 0.001$ . Post hoc tests showed that, irrespective of limb combination, reaction time was fastest when attention was devoted exclusively to the single RT task (276 ms), intermediate when attention was divided equally between both tasks (318 ms), and slowest when attention was focused on the coordination task (343 ms), all  $p < 0.001$ .

Furthermore, there were significant main effects of limb combination,  $F(1.7, 29.4) = 9.65$ ,  $p < 0.001$ , and coordination mode,  $F(1, 17) = 7.82$ ,  $p < 0.05$ .

However, a significant limb combination x coordination mode interaction (see Figure 5B),  $F(2, 34) = 4.33$ ,  $p < 0.05$ , indicated that reaction time during in-phase coordination was faster when the motor task was performed by the upper limbs (299 ms) than by either the contralateral (314 ms) or ipsilateral (318 ms) limb combinations (all  $p < 0.01$ ), whereas probe RT during anti-phase coordination did not differ between the upper (306 ms) and contralateral (311 ms) limb combinations but both were significantly faster than the ipsilateral limb combination (328 ms), (all  $p < 0.05$ ). Comparisons between the coordination modes for each limb combination showed that the mean RT during in-phase coordination was significantly faster than during anti-phase coordination for the upper and ipsilateral limb combinations,  $t(17) = -2.76$ ,  $p < 0.05$ ,  $t(17) = -2.79$ ,  $p < 0.05$ , respectively, but not for the contralateral combination.

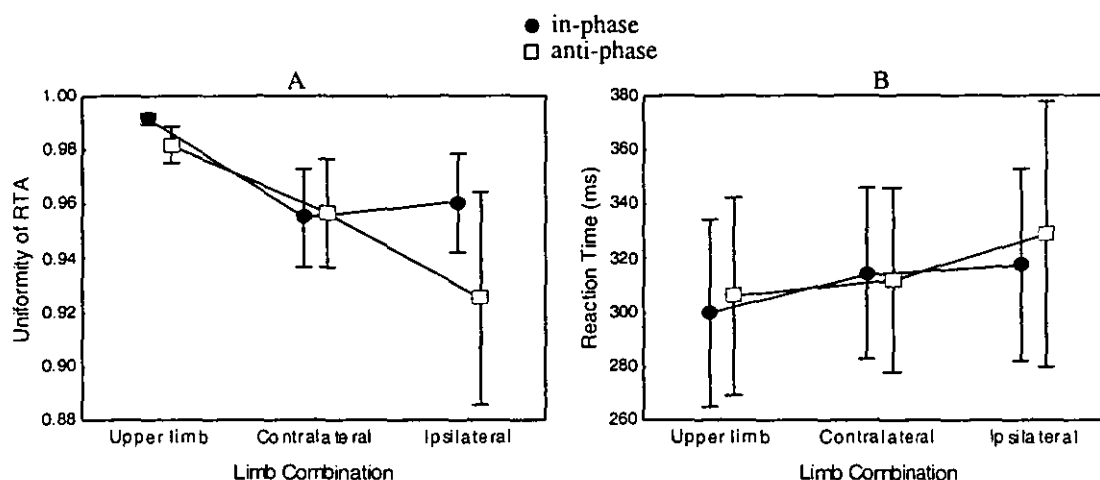


Figure 5. Average performance for in-phase and anti-phase coordination modes as a function of limb combination conditions. (A) Mean uniformity of RTA. (B) Mean vocal RT. Error bars represent 95% confidence intervals.

A significant limb combination  $\times$  attention interaction,  $F(3.6, 61.3) = 4.95$ ,  $p < 0.01$ , reinforced the main effects of the two factors separately, and showed that probe RT was significantly faster during upper limb and contralateral limb coordination than during ipsilateral limb coordination for both dual-task attentional priority conditions.

Overall, the central cost, measured by probe RT, associated with performing the circling task with three different limb combinations was the least for the homologous and the greatest for ipsilateral limb combinations with the contralateral condition showing intermediate cost. In addition, probe RT was influenced by coordination mode for the upper limb and ipsilateral combinations, with the more stable in-phase pattern showing faster probe RTs than the anti-phase coordination pattern. In contrast, no difference in the attentional load associated with maintaining the two coordination modes was evident for the contralateral limb combination.

Across all limb combinations, RT was also significantly faster when sharing attention between tasks than when prioritising the coordination task.

#### 3.4.4 Structural interference during dual-task performance

To examine the extent to which probe RT task responses interfered with the motor coordination task (i.e., structural interference) a moment-by-moment analysis was performed on the AE of RTA, uniformity of RTA and movement frequency deviation data from the interlimb coordination task for each participant (Temprado et al., 1999). Such analysis consisted of inspecting cycle by cycle the subject's movement profile around the occurrence of an auditory probe stimulus – a cycle corresponded to one complete circle of the drawing task, measured from the point on the ongoing circle where the probe stimulus was delivered. Four cycles were calculated, two cycles before and two cycles after the occurrence of a probe stimulus.

A 3 X 2 X 2 X 4 (Limb Combination X Attention X Coordination Mode X Cycle) ANOVA with repeated measures on all factors was carried out on the mean of each dependent variable. The three levels of limb combination were upper limbs, contralateral (left-arm and right leg) and ipsilateral (right-arm and right-leg). Attention consisted of two levels: dual-task with divided attention, and dual-task with priority on the motor task. The two levels of coordination mode were in-phase and anti-phase. The four cycles were -2, -1, +1, +2 – negative and positive values representing the cycles before and after the probe RT stimulus, respectively. ANOVA

results for all dependent variables are summarised in Table 1. However, only significant results involving cycle are reported below.



Table 1. ANOVA Results (*df* and *F* values) for Moment by Moment Analysis for Different Variables (Experiment 1)

	MFD	AE of RTA	UNIF. of RTA
Limb Combination (LC)	$F(2,34) = 1.06$	$F(1.6,27.5) = 6.82^{**}$	$F(1.8,31.0) = 110.02^{***}$
Attention (A)	$F(1,17) = 27.83^{***}$	$F(1,17) = 1.09$	$F(1,17) = 0.45$
Coordination Mode (CM)	$F(1,17) = 19.42^{***}$	$F(1,17) = 35.62^{***}$	$F(1,17) = 32.27^{***}$
Cycle (C)	$F(1.9,33.9) = 39.94^{***}$	$F(2.6,45.6) = 4.01^*$	$F(3,51) = 2.72$
LC x A	$F(1.6,28.8) = 3.65^*$	$F(2,34) = 1.15$	$F(2,34) = 0.04$
LC x CM	$F(1.8,30.8) = 11.38^{***}$	$F(2,34) = 5.29^{**}$	$F(1.5,26.7) = 17.52^{***}$
LC x C	$F(6,102) = 0.70$	$F(6,102) = 1.85$	$F(6,102) = 1.09$
A x CM	$F(1,17) = 2.08$	$F(1,17) = 2.01$	$F(1,17) = 0.40$
A x C	$F(3,51) = 0.85$	$F(3,51) = 0.23$	$F(3,51) = 2.82$
CM x C	$F(3,51) = 1.94$	$F(3,51) = 1.21$	$F(3,51) = 0.15$
LC x A x CM	$F(2,34) = 3.02$	$F(2,34) = 0.54$	$F(2,34) = 0.20$
LC x CM x C	$F(6,102) = 0.91$	$F(6,102) = 0.92$	$F(6,102) = 1.56$
LC x A x C	$F(6,102) = 0.50$	$F(6,102) = 0.22$	$F(6,102) = 1.83$
CM x A x C	$F(3,51) = 0.85$	$F(3,51) = 2.51$	$F(3,51) = 1.69$
LC x A x CM x C	$F(6,102) = 1.23$	$F(6,102) = 1.19$	$F(6,102) = 1.63$

\*  $p < 0.05$     \*\*  $p < 0.01$     \*\*\*  $p < 0.001$

*Movement frequency deviation (MFD).* A significant main effect of cycle,  $F(1.9, 33.9) = 39.94$ ,  $p < 0.001$ , as illustrated in Figure 6, revealed that movement frequency deviation for the first cycle after the presentation of a stimulus (0.091 Hz) was significantly greater than the remaining cycles (-2 = 0.002 Hz; -1 = -0.002 Hz; +2 = 0.008 Hz).

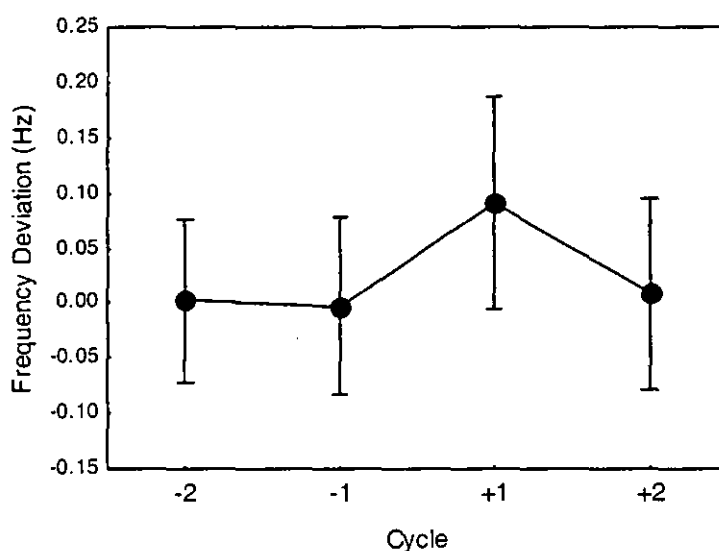


Figure 6. Mean movement frequency deviation across movement cycles before and after probe stimuli. Error bars represent 95% confidence intervals.

*AE of RTA.* A significant main effect of cycle,  $F(2.6, 45.6) = 4.01$ ,  $p < 0.05$ , showed that AE of RTA was significantly smaller for the second cycle (13.6°) before the probe stimulus than for the second cycle (16.2°) after the stimulus. The interaction between coordination mode and cycle was not significant (see Figure 7A).

*Uniformity of RTA.* The main effect of cycle was not significant,  $F(2.9, 50.06) = 2.72$ ,  $p > 0.05$ , nor any of the interactions involving cycle. Figure 7B shows the lack of structural interference from the probe task stimuli on both in-phase and anti-phase coordination modes.

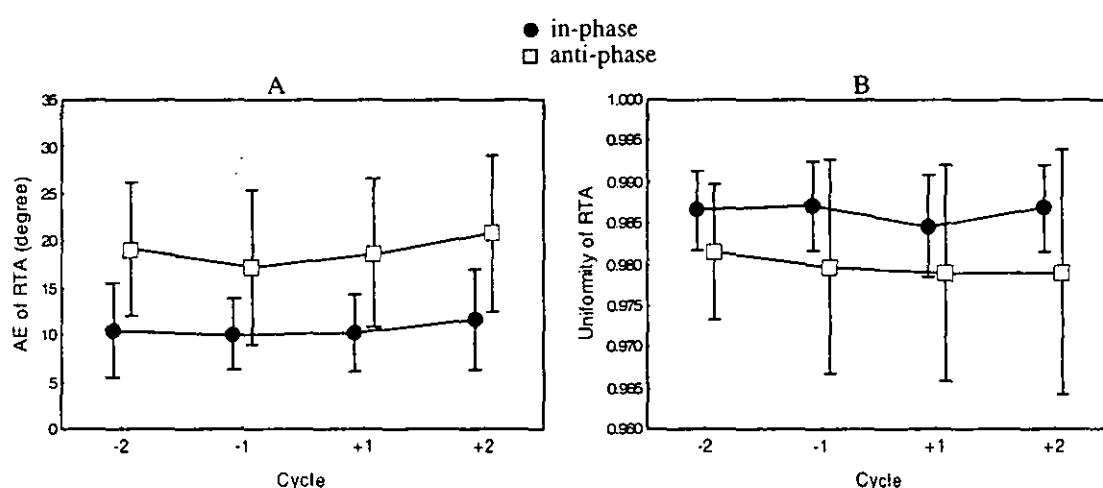


Figure 7. Average performance for in-phase and anti-phase coordination modes across movement cycles before and after probe stimuli. (A) Mean AE of RTA. (B) Mean uniformity of RTA. Error bars represent 95% confidence intervals.

The moment-by-moment analysis showed that probe RT stimulus delivery and associated vocal responses did not significantly perturb either the pattern stability or between-limb synchronisation. There was, however, some evidence that the probe task caused a momentary increase in frequency of the circular movements produced in the circle drawing task.

#### 3.4.5 Effects of attention prioritisation on movement trajectories.

*Aspect ratio.* Analysis of the mean aspect ratio revealed main effects of limb combination  $F(2, 34) = 33.31$ ,  $p < 0.001$ , and coordination mode,  $F(1, 17) = 5.46$ ,  $p <$

0.05. Movement trajectories were more circular in the upper limb combination (0.919), than in the contralateral limb combination (0.891), or the ipsilateral limb combination (0.866), all  $p < 0.01$ . Trajectories produced in the in-phase coordination (0.897) were more circular than in the anti-phase coordination mode (0.886).

Examples of movement trajectories in the upper, contralateral and ipsilateral limb combinations for the in-phase and anti-phase coordination patterns are shown in Figures 8 to 10. The main effect of attention was not significant,  $F(1.9,33.4) = 1.63$ ,  $p > 0.05$ , nor any of the interactions.

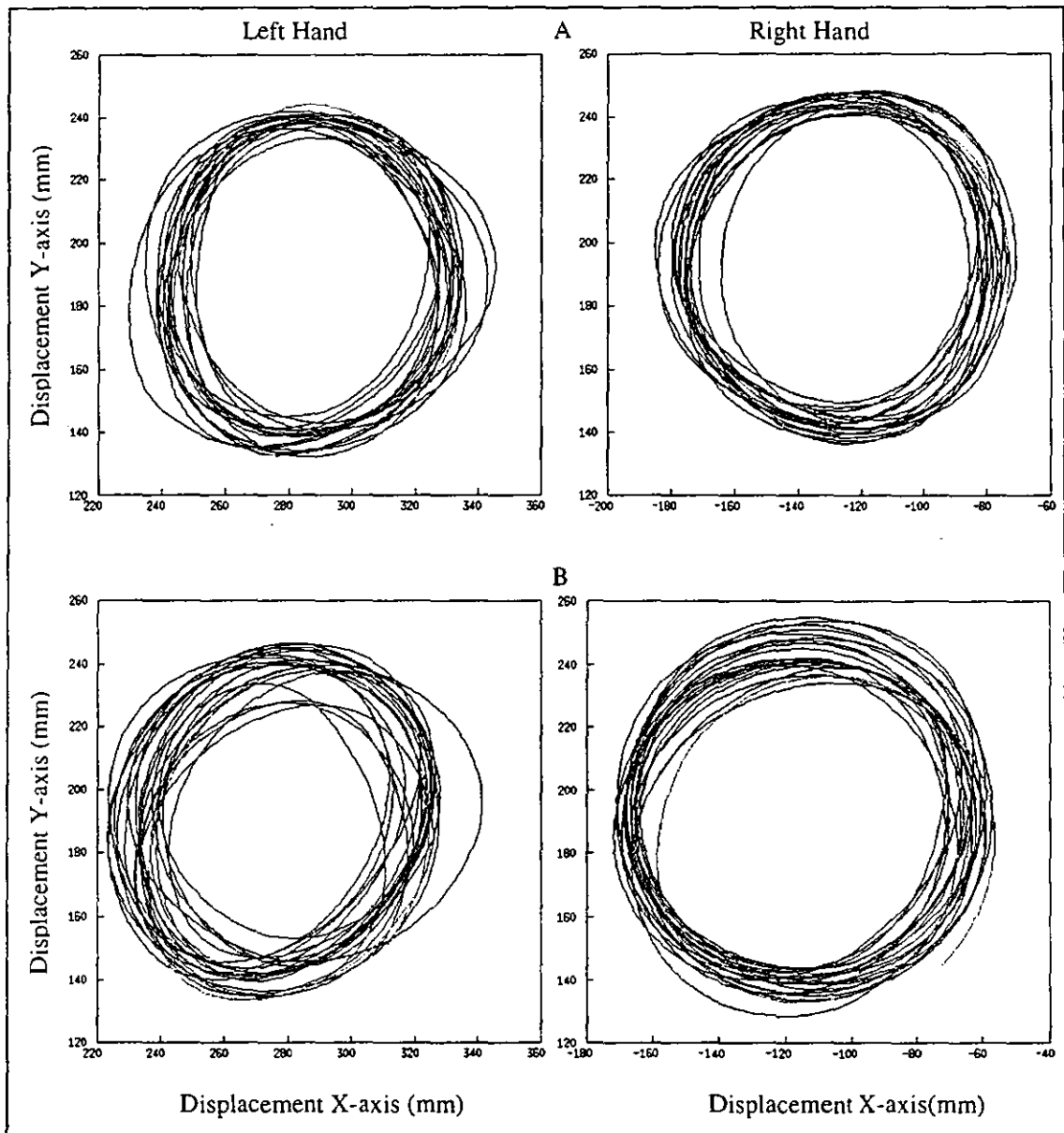


Figure 8. Example of circle drawings for left-hand and right-hand in the upper limb combination condition. (A) In-phase. (B) Anti-phase.

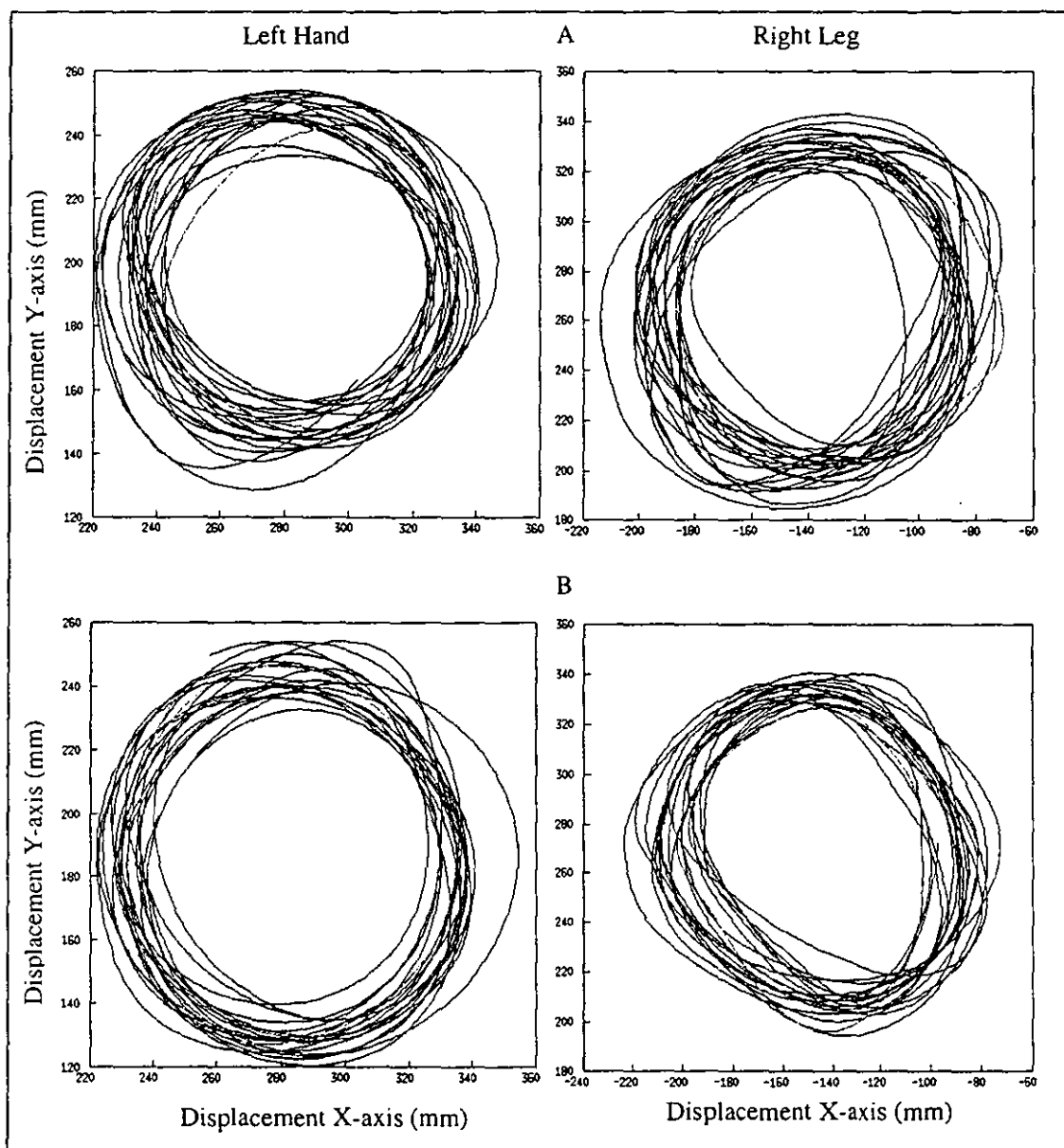


Figure 9. Example of circle drawings for left-hand and right-leg in the contralateral limb combination condition. (A) In-phase. (B) Anti-phase.

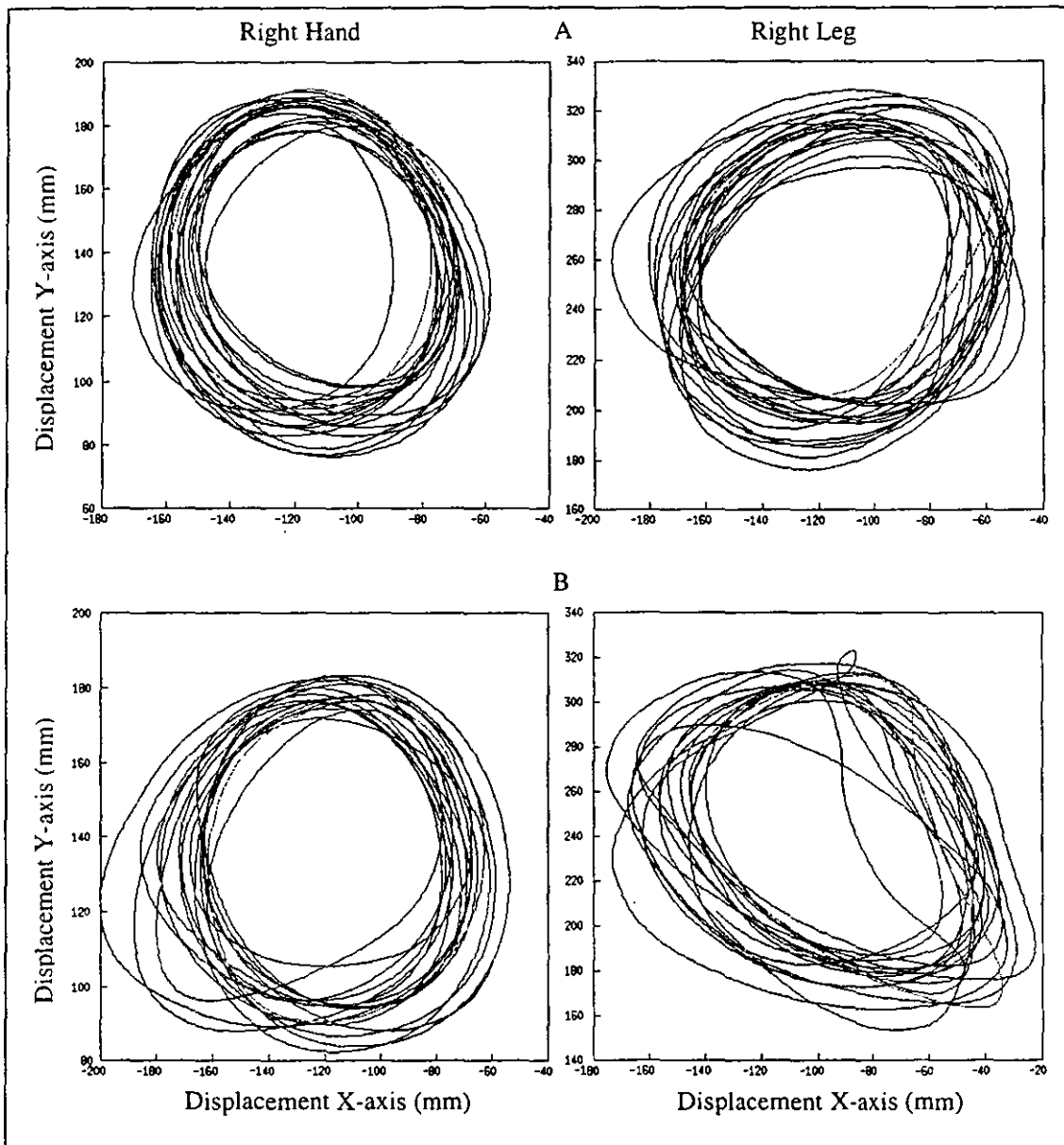


Figure 10. Example of circle drawings for left-hand and right-leg in the ipsilateral limb combination condition. (A) In-phase. (B) Anti-phase.

Differences between limbs in aspect ratio were examined through separate 2 X 3 X 2 repeated measures ANOVAs performed on each of the three limb combinations with two levels of limb type (left- and right-hand for the upper limb combination, hand and leg for the contralateral and ipsilateral combinations), three

levels of attention (single, dual-divided and dual-priority) and two levels of coordination mode (in-phase and anti-phase).

Figure 11A illustrates differences between the limbs in each limb combination. The terms dominant and non-dominant segments employed in Figures 11A,B within each limb combination denote a more and less skilful limb, respectively, when performing the circle drawing task. For homologous limb combination the right arm is the dominant segment and for non-homologous limb combinations involving coordination of an arm and leg the arm is the dominant segment. As expected, for the upper limb combination trajectories produced by the right-hand (0.934) were significantly more circular than those produced by the left-hand (0.903),  $F(1, 17) = 19.99, p < 0.001$ . Furthermore, a main effect of attention,  $F(1.6, 27.2) = 3.69, p < 0.05$ , revealed that movement trajectories exhibited during dual-task with attention priority on coordination (0.914) were significantly less circular than during the single-task (0.925) condition ( $p < 0.05$ ). The ANOVA performed on the contralateral limb combination showed that the left-hand (0.904) produced more circular trajectories than the right-leg (0.878),  $F(1, 17) = 6.63, p < 0.05$ . A similar pattern was evident in analysis of the ipsilateral limb combination with the right-hand (0.886) displaying higher movement circularity than the right-leg (0.845),  $F(1, 17) = 8.93, p < 0.01$ . In addition, for the ipsilateral combination the in-phase coordination mode (0.880) produced more circular movement trajectories than the anti-phase mode (0.851).



*Spatial error.* There were significant main effects of limb combination,  $F(1.7, 30.0) = 51.02, p < 0.001$ , and coordination mode,  $F(1, 17) = 6.20, p < 0.05$ , as well as their interaction,  $F(2, 34) = 5.96, p < 0.01$ . As with the measure of movement circularity (i.e., aspect ratio), the main effect of attention was not significant,  $F(2, 34) = 0.17, p > 0.05$ . Further exploration of the significant limb combination  $\times$  coordination mode interaction showed that the spatial variability exhibited by the upper limb combination (in-phase = 2.73 mm; anti-phase = 2.97 mm) was significantly smaller than the contralateral (in-phase = 4.01 mm; anti-phase = 3.93 mm) and ipsilateral limb combinations (in-phase = 3.98 mm, anti-phase = 4.23 mm), all  $p < 0.001$ . The in-phase coordination mode was significantly less variable than anti-phase mode in the upper,  $t(17) = -3.60, p < 0.01$ , and ipsilateral limb combinations,  $t(17) = -2.20, p < 0.05$ , but not in the contralateral combination.

To examine differences between the limbs, 2 X 3 X 2 (Limb Type X Attention X Coordination Mode) ANOVAs with repeated measures were conducted on the spatial error measure in each limb combination. Figure 11B illustrates differences between the limbs in each limb combination. As expected, for the upper limb combination the spatial variability of movement trajectories in the right-hand (2.64 mm) was significantly smaller than in the left-hand (3.05 cm),  $F(1, 17) = 10.78, p < 0.01$ . Furthermore, a main effect of coordination mode,  $F(1, 17) = 13.02, p < 0.01$ , indicated that the spatial variability for the in-phase coordination mode (2.73 mm) was smaller than the anti-phase (2.97 mm). For both the contralateral (hand = 3.42 mm, leg = 4.52 mm) and ipsilateral (hand = 3.19 mm, leg = 5.03 mm) limb

combination analyses, spatial variability was significantly smaller for the hand than for the leg  $F(1,17) = 28.68$ ,  $p < 0.001$ , and  $F(1,17) = 32.84$ ,  $p < 0.001$ , respectively. In addition, the ANOVAs for each of the non-homologous limb combinations revealed a significant limb type  $\times$  coordination mode interaction,  $F(1, 17) = 10.08$ ,  $p < 0.01$ ,  $F(1, 17) = 18.53$ ,  $p < 0.001$ , respectively. For the contralateral limb combination, post hoc tests conducted on the interaction indicated that spatial error for the in-phase mode (4.66 mm) was greater than the anti-phase mode (4.38 mm,  $p < 0.05$ ) for the right-leg. In contrast, no difference between coordination modes was evident for the left-hand (in-phase = 3.36 mm; anti-phase = 3.48 mm,  $p > 0.05$ ). A similar pattern was obtained for the ipsilateral limb combination, with spatial error greater for the anti-phase mode (5.35 mm) than for the in-phase mode (4.70 mm,  $p < 0.001$ ) for the right-leg, but no significant differences between coordination modes for the right-hand (in-phase = 3.27 mm; anti-phase = 3.11 mm,  $p > 0.05$ ).

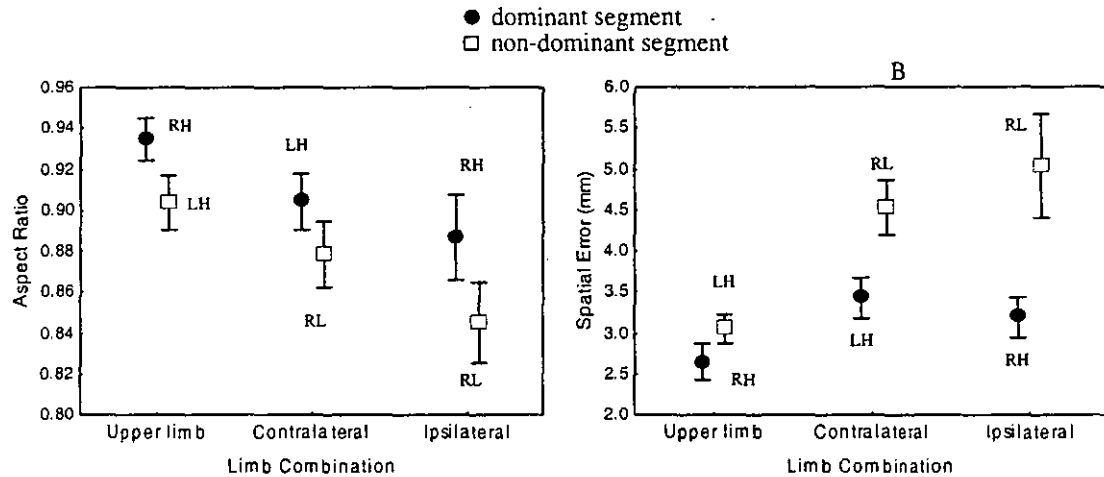


Figure 11. Average performance for dominant segment and non-dominant segment as a function of limb combination conditions. (A) Mean aspect ratio. (B) Mean spatial error. Error bars represent 95% confidence intervals. RH (right-hand); LH (left-hand); RL (right leg).

A particularly interesting finding in the analysis of the spatial aspects of circle drawing performance was that attention directed towards the coordination task did not influence the spatial measures (i.e., aspect ratio and spatial error) of interlimb coordination, indicating a possible dissociation between the temporal and spatial parameters of the coordination task. In addition, results for both spatial error and aspect ratio measures showed decrements in performance from upper limbs to contralateral and to ipsilateral limb combinations, mainly during the anti-phase coordination mode.

### 3.5 Discussion

Recently a number of studies of bimanual coordination have established a link between coordination dynamics and central processing activity. The present study investigated whether the co-variation of coordination pattern stability and attentional

demands would also be observed in tasks requiring the coordination of upper and lower limbs, thereby reflecting a general principle by which the central nervous system controls coordinated behaviour. To examine this question, a dual-task procedure was used in which participants moved their upper and lower limbs around circle templates while responding to randomly presented auditory probe stimuli. Performance tradeoffs associated with the allocation of attentional resources were manipulated by having participants focus on different aspects of the dual-task situation.

### 3.5.1 Effects of attentional prioritisation on the stability of coordination patterns

The first aim of the study was to examine whether similar effects of attentional prioritisation on coordination stability observed for single-joint bimanual movements would be evident in the coordination of upper and lower limb multisegmental movements. The results indicated that attentional focus directed to the coordination task significantly increased coordination stability (i.e., uniformity of RTA) across all limb combinations relative to the condition in which attention was divided equally between the two tasks. Consistent with previous research (e.g., Temprado et al., 1999) prioritising coordination stability involved a central cost in terms of an increase in probe RT. Importantly, the levels of temporal accuracy and stability obtained in the dual-task trials when the coordination task was prioritised were similar to those obtained during single-task trials, indicating that participants were able to adhere to the task priority instructions.

In contrast, dividing attention between the coordination and RT tasks resulted in a significant reduction in the accuracy and stability of interlimb coordination. The effect of attentional focus on the performance of the contralateral and ipsilateral limb combinations was more pronounced than on the performance of the upper limb combination. However, prioritising attention to the coordination pattern did not annihilate the inherent differences in the stability of the coordination dynamics across the three limb combinations. The strong attentional effects evident for the less stable limb combinations suggest that prioritisation of coordination task strengthen the coupling between the limbs (Schöner & Kelso, 1988).

### 3.5.2 Central cost of stabilising interlimb coordination

The second aim of the study was to determine whether a relationship between coordination stability and central cost would be observed across the limb combinations and coordination modes tested in the present study. As shown in Figures 5A and 5B, the decrement in anti-phase coordination stability from upper limb to contralateral to ipsilateral limb combinations was associated with an increase in probe RT, with the fastest RT evident during upper limb coordination, intermediate in the contralateral and the slowest during ipsilateral limb coordination. A similar relationship was evident for the in-phase coordination mode with the more stable upper limb combination being associated with faster probe RTs than both contralateral and ipsilateral limb combinations. From a dynamical systems perspective, differences in stability among coordination systems reflect the coupling

strength of the oscillators involved in the coordination. Biophysical properties, for example, have been suggested to account for the weaker coupling between upper and lower limbs (Kelso & Jeka, 1992). The co-variation between coordination stability and central cost in the limb combinations tested adds further support to the view that the attentional resources devoted by the CNS to a task depends on the coupling strength between the moving segments.

It is well established for upper limb coordination (Temprado et al., 1999) that movements performed in the in-phase pattern (i.e., involving the simultaneous activation of homologous muscles) are more stable and require less attentional resources (i.e., shorter probe RT) to maintain than the anti-phase pattern (i.e., involving simultaneous activation of non-homologous muscles). The expected relationship between coordination mode stability and central cost was evident in the present study for upper limb coordination.

For the coordination of non-homologous limb combinations, previous research has shown that isodirectional (i.e., in-phase) movements are more stable than non-isodirectional (i.e., anti-phase) movements. This finding is consistent with the view that movement direction is coded in the CNS by a population of neurons (Georgopoulos, 1991; Georgopoulos, Taira, & Lukashin, 1993) and that the system has difficulty in simultaneously specifying different directions for limb movements (Swinnen et al., 1997). If the co-variation between pattern stability and attentional load also applies to the coordination of non-homologous limbs, then in-phase patterns should be associated with lower central cost (i.e., probe RT) than anti-phase patterns.

As predicted, when ipsilateral limbs were coordinated isodirectional (in-phase) movements exhibited greater stability and lower central cost than non-isodirectional (anti-phase) movements.

For the contralateral limb combination, however, the in-phase and anti-phase coordination modes exhibited equivalent levels of stability. One possible explanation is that the preference, observed in bimanual movements, for simultaneously moving limb pairs towards and away from the body midline termed the egocentric constraint (Swinnen et al., 1997)<sup>2</sup>, operated to stabilise contralateral limb movements in the anti-phase (non-isodirectional) pattern. There is growing awareness that interlimb coordination stability depends on the interaction between a variety of constraints operating on the coordination system (e.g., Carson & Kelso, 2004). For example, recent research on bimanual coordination has shown that egocentric, directional (allocentric), and muscular (homologous muscular activation) constraints are dissociable and, depending on the task context, interact to either facilitate or reduce coordination stability (Park et al., 2001; Temprado et al., 2003). Furthermore, movement direction may not be the only explanation for the low stability exhibited in the performance of the anti-phase (non-isodirectional) pattern when ipsilateral limbs were coordinated, as a recent study of H-reflex modulation in the forearm indicated that muscular contraction, rather than foot kinematics, of the lower limb is synchronised with the upper limb (Cerri, Borroni, & Baldissera, 2003). Of particular

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<sup>2</sup> In previous studies of bimanual coordination the egocentric constraint has been also referred to as the mirror-image or the iso-muscular constraint (Swinnen, 2002; Swinnen et al., 1997). Here we use the term egocentric to refer to direction of movement with respect to the longitudinal axis of the body without reference to muscular constraints

significance in the present study, however, was the finding that the equivalence in stability between in-phase and anti-phase coordination modes in the contralateral limb combination was associated with equivalent probe RTs for the two patterns, further confirming the strong link between pattern stability and central costs.

In the present study the association between central cost and coordination dynamics was observed using a vocal RT task. Vocal RT as a secondary probe task was deliberately employed to ensure that attentional load would occur primarily at the central level. With respect to the degree of structural interference on the coupling between the limbs, the results obtained here differed from those previously found (Temprado et al., 1999, 2001) using motor RT tasks involving either feet or fingers. Employing a moment-by-moment analysis, Temprado and colleagues (1999; 2001) detected a transient perturbation on coordination stability in the first cycle of pronation-supination motion at the very moment of response to probe RT stimulus. In addition, they found that attentional prioritisation minimised the transient perturbation on coordination stability in the first cycle following the response to probe RT stimulus, irrespective of whether the RT response was with the foot or hand. The authors suggested that interference at a central rather than a peripheral level (i.e., mechanical interactions) was responsible for the perturbation to the bimanual coordination task.

In contrast, both the present study and Elder (2001a), showed that a vocal probe RT task did not perturb the coupling between the limbs (i.e., AE of RTA and uniformity of RTA) in the circle drawing task (see Figure 7A,B). This finding,



therefore, supports the view that in the dual-task situation a vocal probe RT task provides a more pure measure of attentional cost at the central level. There was, however, in the moment-by-moment analysis some evidence of a transient perturbation of movement frequency in the first cycle after presentation of a probe stimulus for both in-phase and anti-phase modes (see Figure 6). The perturbation of movement frequency was expressed as a transient increase in the movement rate of the interlimb coordination. It appears that structural interference, that is the intrusion of the probe RT response on interlimb coordination performance, may influence on two different levels: (a) at a peripheral level causing transient increases in movement frequency which cannot be prevented by attentional prioritisation; (b) at a central level producing decrements in coordination pattern stability which can be minimised significantly through attentional prioritisation (see Temprado et al., 1999).

Determining the neural basis of structural interference during the simultaneous performance of rhythmic interlimb coordination and discrete probe RT tasks is an important issue for understanding the dual-task situation and was examined in the second part of this research.

### 3.5.3 Spatial aspects of the circle drawing task

In recent years, the circle drawing task has been used extensively to examine the temporal and spatial properties of interlimb coordination (e.g., Carson et al., 1997; Franz & Packman, 2004; Semjen et al., 1995; Summers et al., 1995). Although the spatial and temporal dimensions appear intertwined in this task, there is some

evidence that they may be independently controlled. For example, applying tendon vibration to one arm during bimanual circle drawing disrupts the temporal synchronisation between the hands but not the circularity of the trajectories produced by the two hands (Verschueren, Swinnen, Cordo, & Dounskaia, 1999a). Proprioceptive information, therefore, appears to mediate the temporal synchronisation between the limbs. In contrast, looking at a mirror reflection of one hand during bimanual circling influences the spatial but not the temporal coupling between the hands (Franz & Packman, 2004; Summers, Wade-Ferrell, & Kagerer, 2003).

There is also research with callosotomy patients that supports the view that spatial and temporal constraints on bimanual coordination involve separable mechanisms (Franz, Eliassen, Ivry, & Gazzaniga, 1996). Specifically, it was argued that the spatial constraints evident in bimanual tasks result from interhemispheric interactions via the corpus callosum, whereas the temporal aspects are controlled subcortically. In the present study, when participants prioritised the coordination task they were instructed to concentrate on the temporal coupling between the hands and feedback was given only on the temporal aspects of the task (i.e., frequency, relative phase, uniformity). A question of interest, therefore, was whether improvements in the temporal accuracy and stability of interlimb coordination through attentional prioritisation (see Figures 4A,B) would be accompanied by changes in the spatial control of the hands.

Previous research using bimanual circle drawing has shown that directing attention to one limb affected both temporal (relative phase) and spatial (aspect ratio, circle size) task parameters (Swinnen et al., 1996; Wuyts et al., 1996). In the present study, in contrast, directing attention to the temporal coupling between the limbs, rather than to a specific limb, influenced that dimension but did not affect the circularity or variability of the movement trajectories produced by each hand (i.e., aspect ratio, spatial error). These results add further support to the view that the temporal and spatial dimensions may be independently controlled and suggest that attention may constitute an intervening variable capable of dissociating the two task parameters. Whether attentional prioritisation to the spatial aspects of circle drawing can selectively influence that component of the task is further explored in the next study.

### **3.6 Conclusion**

Recently, the interplay between the coordinative activity of the central nervous system and coordination dynamics has been revealed through a dual-task paradigm involving a primary rhythmic coordination task and a secondary probe RT task. The present study extended previous research by establishing that the co-variation between pattern stability and central cost evident for upper limb coordination is also observed for the coordination of an arm and leg. Stabilising coordination patterns through attentional prioritisation was shown to incur measurable central cost that was associated with the dynamics of coordinating movement patterns according to the

coupling strength between the moving limbs. As such, our results provide further evidence that probe RT offers an accurate measure of the coordination activity of the central nervous system associated with the collective variable, relative phase and its stability.

## Chapter 4 Experimental Study 2

### 4.1 Spatial and Temporal Interactions in Interlimb Coordination

As previous studies of interlimb coordination have used relatively simple single degree-of-freedom movements (e.g., forearm pronation-supination) the focus has predominantly been on the temporal interaction between the two limbs. It has been observed that tapping simple rhythms with the fingers (e.g., 1:1, 1:2 ratio), for example, is quite easy to perform, whereas producing polyrhythmic tapping (e.g., 2:3, 2:5 ratio) requires great effort to prevent the temporal coupling of the two conflicting motor sequences (Klapp, 1979; Summers & Kennedy, 1992). On the other hand, it has also become evident from studies examining the spatial interactions of movement trajectories in interlimb coordination that dissimilar spatial trajectories assigned to each limb limit overall movement performance. Franz and colleagues (1991), for example, demonstrated a mutual assimilation effect in hand movement trajectories when participants were required to simultaneously draw continuous vertical lines with one hand and circles with the other: circles became more like lines and lines became more circular. The spatial interference of one hand on the other but with a tight temporal relationship indicates that the spatial dimension plays an important role in movement control of a bimanual task (see also Bogaerts & Swinnen, 2001; Franz, 1997).

In Experiment 1, focusing attention on the temporal coupling between the limbs during performance of the coordination task did not affect the spatial aspects

(i.e., movement circularity) of the circles produced by each limb but it did influence temporal dimensions of the coordination task (i.e., relative phase and stability of relative phase). Even in a task such as interlimb circle drawing where temporal and spatial dimensions appear to be strongly intertwined, these results add further support to the view that both spatial and temporal dimensions of interlimb coordination may be independently controlled (Franz et al., 1996).

Research involving people in whom the corpus callosum had been surgically sectioned as a consequence of intractable epilepsy has indicated that, at least for discrete movements, constraints related to spatial and temporal components of interlimb coordination tasks may be controlled at different levels of the CNS (Franz et al., 1996). Specifically, spatial components involve callosal connections, whereas temporal aspects involve subcortical structures, primarily the cerebellum. In contrast, for continuous interlimb coordination the control of both spatial and temporal components appears to depend on interhemispheric connections across the corpus callosum (Kennerley, Diedrichsen, Hazeltine, Semjen, & Ivry, 2002). There is behavioural evidence, however, suggesting that both temporal and spatial components of interlimb coordination may operate with some degree of independence. In a study of the effects of tendon vibration applied to the dominant arm during bimanual circle drawing, the results suggested that whereas the spatial characteristics of arm movements seem to be controlled unilaterally, the temporal characteristics of interlimb coordination appear to be controlled by proprioceptive information from both limbs (Verschueren et al., 1999a). The present study, therefore, examined the

extent to which the spatial characteristics of the circle drawing task could be independently manipulated from the temporal aspects of the task.

## **4.2 Aims of the study and predictions**

Three specific questions were addressed in the present study. The first was whether the relationship between stability and central cost observed in Experiment 1 would be replicated in the present study when attention is directed to the spatial aspects of the interlimb circle drawing task. In line with the results obtained in Experiment 1, it was expected that coordinating non-homologous limb combinations would demand more attentional resources than coordinating homologous limb combinations. The second question related to whether dissociation between the spatial and temporal components of the circling task would occur when attentional focus is directed to the spatial dimension. In Experiment 1, the temporal coupling between the limbs was modulated according to the amount of attention devoted to the temporal dimension without affecting the spatial aspects of the coordination task. If the spatial and temporal components of the circling task are independently specified, then directing attentional focus to the spatial dimension should influence the quality of the circular trajectories produced but not the temporal coupling between the limbs. The third question related to whether attention directed to the spatial aspects of circle drawing task would abolish the asymmetrical performance between the limbs observed in Experiment 1. There is some evidence that visual attention towards the non-dominant hand improves spatial performance of this hand almost to a similar level of the dominant hand. It was

expected that attentional focus to spatial dimension of interlimb coordination would annihilate the inherent asymmetry performance between the limbs.

### **4.3 Method**

#### **4.3.1 Participants**

Eighteen volunteers (3 men, 15 women) aged between 18 and 49 (mean = 27 years), from the University of Tasmania took part in the experiment. All participants were naive to the purpose of the study. Selection procedure regarding the manual and pedal preference followed the previous experiment (see Experiment 1). Written informed consent was obtained prior to participation in the study. Ethics approval for the study was obtained from the University of Tasmania Human Research Ethics Committee.

#### **4.3.2 Apparatus and Procedure**

A similar experimental set up and procedure to Experiment 1 was employed, with the exception that attention focus was directed to the spatial characteristics of the circle drawing task (i.e., producing perfect circles with the two hands). To ensure that participants focused on the spatial aspects of the task, in addition to their mean RT to the auditory probe stimuli, feedback was also given on the aspect ratio and spatial error measures of performance. Although the spatial measures of performance were available for each limb separately, to avoid overloading participants only one aspect ratio and spatial error score (i.e., the lowest aspect ratio and highest spatial error achieved) was given as feedback after each trial. However, participants were not informed which limb produced these values. This was done to ensure that participants



would attempt to do their best on both limbs on the next trial. Mean movement frequency was also returned to the participants to assist in the maintenance of the required frequency.

#### 4.3.3 Data reduction and dependent measures

Data were reduced and analysed in the same manner as in the previous experiment (see Experiment 1).

### 4.4 Results

The dependent variables were analysed by means of a 3 X 3 X 2 (Limb Combination X Attention X Coordination Mode) ANOVA with repeated measures on all factors. The three levels of limb combination were upper limbs, contralateral (left-arm and right-leg) and ipsilateral (right-arm and right-leg). The three levels of attention were single-task, dual-task with divided attention, and dual-task with priority on the coordination task. The two levels of coordination mode were in-phase and anti-phase. Data pertaining to both limbs in each limb combination were combined for statistical analysis of aspect ratio and spatial error. Additional analyses were conducted for aspect ratio and spatial error to examine differences between the limbs for each limb combination.

#### 4.4.1 Conformity to required movement frequency

*Movement frequency deviation.* The mean of movement frequency deviation across participants was -0.02 Hz (range -0.24 to 0.15 Hz), indicating that participants conformed to the required pacing (i.e., 1 Hz).

#### 4.4.2 Effects of attentional prioritisation on the spatial aspects of the coordination task

*Aspect ratio.* There were significant effects of limb combination,  $F(2,34) = 30.43$ ,  $p < 0.001$ , attention,  $F(1.8,31.0) = 6.91$ ,  $p < 0.01$ , and a limb combination X coordination mode interaction,  $F(2,34) = 9.84$ ,  $p < 0.001$ . For the main effect of attention, post hoc tests showed that movement trajectories were significantly less circular in the dual-task divided attention condition (0.891) than in the single-task (0.900) and dual-task prioritising coordination (0.897) conditions (all  $p < 0.05$ ), which did not differ significantly (see Figure 12).

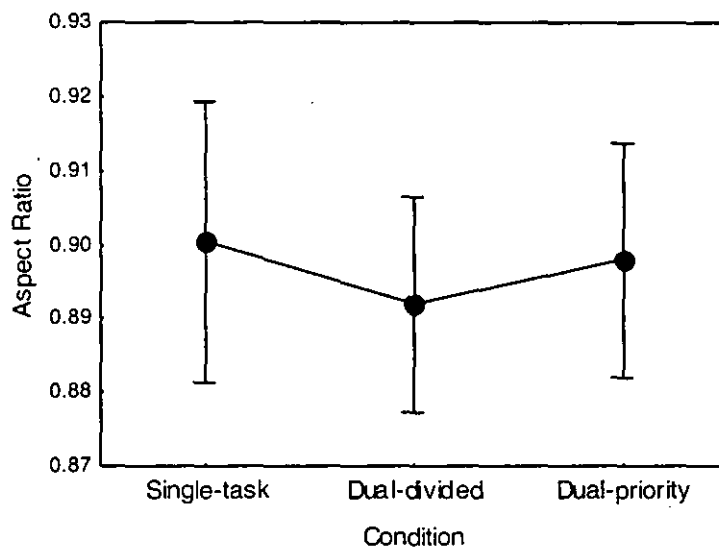


Figure 12. Mean aspect ratio for single-task, dual-task with divided attention, and dual-task with attentional priority on coordination task. Error bars represent 95% confidence intervals.

Subsequent analyses of the two-way interaction (see Figure 13A) showed that movement trajectories produced by the upper limbs during the in-phase coordination (0.920) were significantly more circular than both the contralateral (0.898) and ipsilateral (0.885) limb combinations (all  $p < 0.05$ ), no significant difference was evident between the contralateral and ipsilateral limb combinations. For the anti-phase coordination mode movement trajectories were significantly different among all limb combination conditions, with the upper limb combination evidencing the highest aspect ratio (i.e., most circular) (0.923) followed by the contralateral (0.901), and then the ipsilateral limb combination (0.851) (all  $p < 0.05$ ). Furthermore, movement trajectories during in-phase coordination were significantly more circular than during anti-phase coordination for the ipsilateral limb combination,  $t(17) = 3.85$ ,  $p < 0.01$ , but not for the upper and contralateral limb combinations.

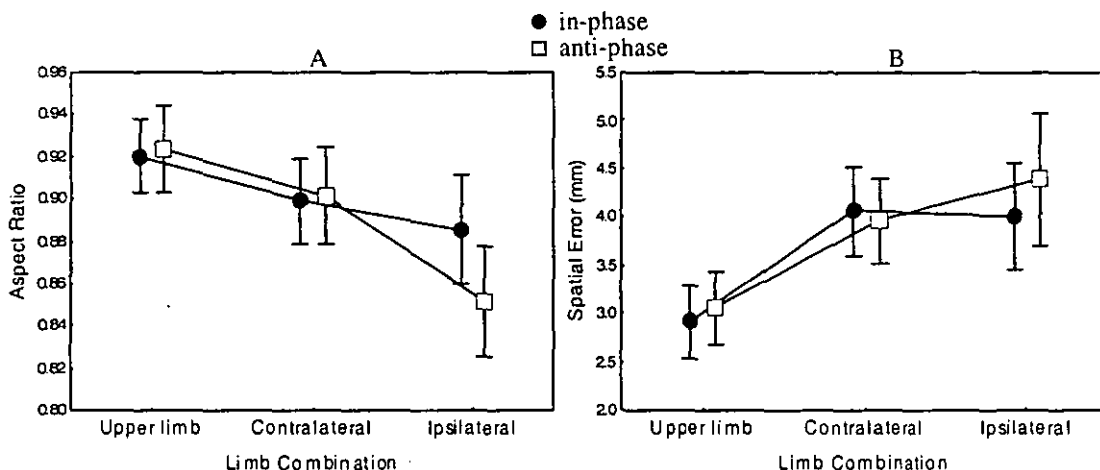


Figure 13. Average performance for in-phase and anti-phase coordination modes as a function of limb combination conditions. (A) Mean aspect ratio. (B) Mean spatial error. Error bars represent 95% confidence intervals.

Comparisons between the limbs (i.e., left-hand vs. right-hand, or hand vs. leg) were examined through separate 2 X 3 X 2 repeated measures ANOVAs performed on each of the three limb combinations with two levels of limb type (left-hand and right-hand for the upper limb combination, hand and leg for the contralateral and ipsilateral combinations), three levels of attention (single, dual-divided and dual-priority), and two levels of coordination mode (in-phase and anti-phase). Figure 14A shows aspects ratios for the dominant and non-dominant segment for each limb combination averaged over attention and coordination mode conditions. Of particular note was that there was no significant effect of limb type in any of the analyses (upper limb: left-hand = 0.918, right-hand = 0.925; contralateral: left-arm = 0.900, right-leg = 0.899; ipsilateral: right-arm = 0.879, right-leg = 0.857, all  $p > 0.05$ ). In addition, for the contralateral limb combination there was a main effect of attention,  $F(1.7, 29.6) = 3.84$ ,  $p < 0.05$ , produced by a significant decrement in dual-task performance when attention was divided (0.894) compared to single-task performance (0.904). Dual-task with attentional priority (0.901) did not differ significantly from any of the attentional conditions. The only other significant effect was for coordination mode in the ipsilateral limb combination (in-phase = 0.885; anti-phase = 0.851),  $F(1, 17) = 13.60$ ,  $p < 0.01$ .

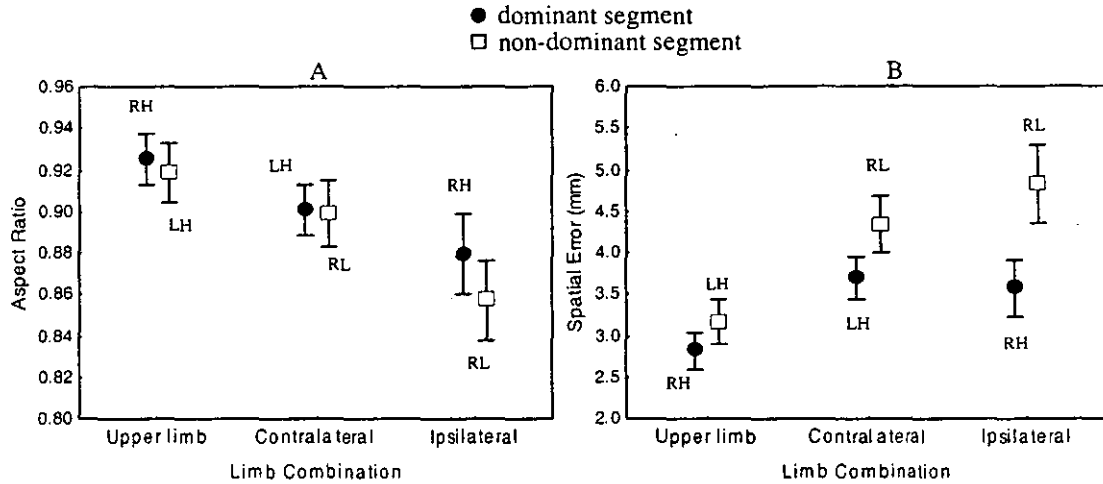


Figure 14. Average performance for dominant segment and non-dominant segment as a function of limb combination conditions. (A) Mean aspect ratio. (B) Mean spatial error. RH (right-hand); LH (left-hand); RL (right leg). Error bars represent 95% confidence intervals.

*Spatial error.* There were significant main effects of limb combination,  $F(1.8, 30.7) = 59.94, p < 0.001$ , coordination mode,  $F(1, 17) = 11.64, p < 0.01$ , as well as their interaction,  $F(1.9, 33.4) = 11.16, p < 0.001$ . Similar to the pattern observed for the aspect ratio, the limb combination X coordination mode interaction (see Figure 13B) showed that during in-phase coordination the upper limb combination (2.91 mm) exhibited significantly lower spatial variability than both the contralateral (4.05 mm) and ipsilateral (4.00 mm) limb combinations (all  $p < 0.001$ ). During anti-phase coordination, however, the variability of movement trajectories differed significantly among the three limb combinations, with the upper limb combination (3.05 mm) exhibiting the lowest variability, the ipsilateral combination (4.38 mm) the highest, and the contralateral limb combination (3.96 mm) an intermediate level of variability (all  $p < 0.05$ ). Furthermore,  $t$ -tests indicated that the in-phase coordination was less

variable than anti-phase coordination for the upper,  $t(17) = -2.87, p < 0.05$ , and ipsilateral,  $t(17) = -4.11, p < 0.001$  limb combinations, but not for the contralateral limb combination.

As with the aspect ratio measure,  $2 \times 3 \times 2$  (Limb Type  $\times$  Attention  $\times$  Coordination Mode) ANOVAs with repeated measures were carried out on the spatial error in each limb combination to particularly examine differences between the limbs (see Figure 14B). For the upper limb combination the spatial variability of movement trajectories produced by the right-hand (2.81 mm) was significantly smaller than those produced by the left-hand (3.15 mm),  $F(1,17) = 7.39, p < 0.05$ . A main effect of attention,  $F(2,34) = 7.47, p < 0.01$ , showed that spatial error variability was significantly greater during dual-task divided attention (3.06 mm) compared with both single-task (2.96 mm) and dual-task prioritising coordination task (2.92 mm) (all  $p < 0.05$ ), which did not differ from each other. For the contralateral limb combination, there was only a significant main effect for limb type,  $F(1,17) = 16.23, p < 0.001$ , indicating greater spatial error for the right-leg than the left-hand.

For the ipsilateral limb combination, there were significant main effects of limb type,  $F(1,17) = 32.8, p < 0.001$ , and coordination mode,  $F(1,17) = 16.96, p < 0.001$ , as well as significant interactions for limb type  $\times$  attention,  $F(2,34) = 3.96, p < 0.05$ , and limb type  $\times$  coordination mode,  $F(1,17) = 5.99, p < 0.05$ . Simple effect analyses of the interaction between limb type and attention indicated that both for the right-hand (single-task = 3.48 mm; dual-divided = 3.56 mm; dual-priority = 3.66 mm) and the right-leg (single-task = 4.83 mm; dual-divided = 4.92 mm; dual-priority =

4.72 mm) spatial error did not differ across attention conditions. Rather the interaction only indicated a significant lower spatial error for the right-hand than the right leg.

The interaction between limb type and coordination mode showed that whereas significant differences between the in-phase and anti-phase coordination modes were evident for the right-leg (in-phase = 4.50 mm; anti-phase = 5.14 mm,  $p < 0.001$ ), spatial error between coordination modes did not differ for the right-hand. Overall, spatial error variability was significantly lower in the right-hand than in the right-leg ( $p < 0.001$ ).

Of primary importance was the finding for the aspect ratio measure that movement circularity was modulated by attentional focus, whereas the variability of the movement trajectories was not affected by attentional focus.

#### 4.4.3 Effects of attentional prioritisation on temporal coupling of the coordination task

*AE of RTA.* There were significant main effects of limb combination,  $F(1.5, 25.8) = 29.97$ ,  $p < 0.001$ , and coordination mode,  $F(1, 17) = 51.36$ ,  $p < 0.001$ , as well as their interaction,  $F(1.2, 21.4) = 18.93$ ,  $p < 0.001$ . It is worth noting that attention did not achieve any level of significance,  $F(2, 34) = 0.23$ ,  $p > 0.05$ . This result is of particular importance as it directly relates to the question of whether changes in spatial components of interlimb circle drawing task would promote changes in the temporal relationship between the hands.

Further analyses of the two-way interaction (see Figure 15) showed that for in-phase coordination, the upper limb combination ( $5.5^\circ$ ) was significantly more accurate than both the contralateral ( $15.4^\circ$ ) and ipsilateral ( $13.6^\circ$ ) limb combinations (all  $p < 0.01$ ). For anti-phase coordination, the upper ( $17.5^\circ$ ) and contralateral ( $19.2^\circ$ ) limb combinations were significantly more accurate than the ipsilateral limb combination ( $55.5^\circ$ , all  $p < 0.001$ ). Comparisons between coordination modes within each limb combination indicated that the in-phase pattern was produced more accurately than the anti-phase pattern in both the upper and ipsilateral limb combinations,  $t(17) = -4.72, p < 0.001$  and  $t(17) = -5.82, p < 0.001$ , respectively. The coordination modes did not differ in accuracy in the contralateral limb combination.

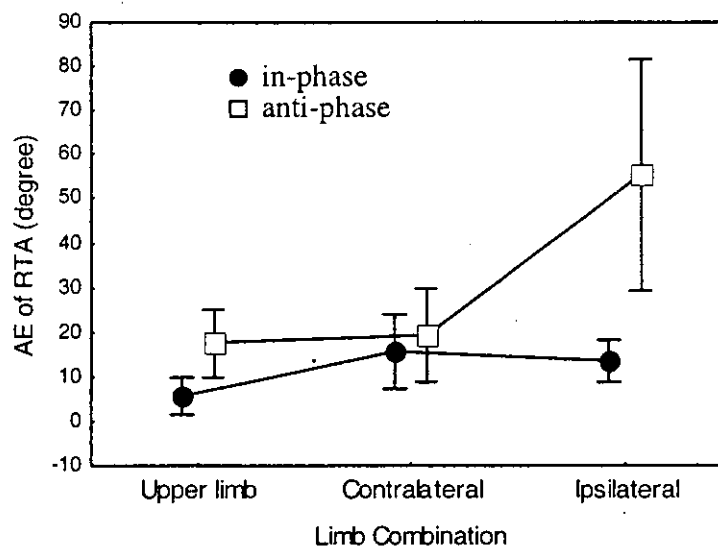


Figure 15. Mean of AE of RTA for in-phase and anti-phase coordination modes as a function of limb combination conditions. Error bars represent 95% confidence intervals.



*Uniformity of RTA.* The ANOVA yielded significant main effects of limb combination,  $F(1.9, 32.3) = 88.68, p < 0.001$ , attention,  $F(2, 34) = 5.53, p < 0.01$ , and coordination mode,  $F(1, 17) = 69.72, p < 0.001$ . There were also significant interactions between attention x coordination mode,  $F(2, 34) = 4.28, p < 0.05$ , and limb combination x coordination mode,  $F(1.1, 20.1) = 21.39, p < 0.001$ .

The significant interaction between attention by coordination mode (see Figure 16) revealed that the stability of the in-phase pattern was not affected by attention focus,  $F(2, 34) = 0.97, p > 0.05$ . In contrast, the anti-phase coordination mode,  $F(2, 34) = 3.76, p < 0.05$ , was significantly less stable when attention was divided between the two tasks (0.890) than when the coordination task was prioritised (0.920,  $p < 0.05$ ). The single-task condition did not differ significantly from either dual-task condition. Thus, the main effect of attention was mainly accounted for by the anti-phase coordination mode. Furthermore, differences between the in-phase and anti-phase coordination modes were evident for each attention condition: single,  $t(17) = 5.40, p < 0.001$ ; dual-task with divided attention,  $t(17) = 5.80, p < 0.001$ ; and dual-task with prioritisation,  $t(17) = 4.64, p < 0.001$ .

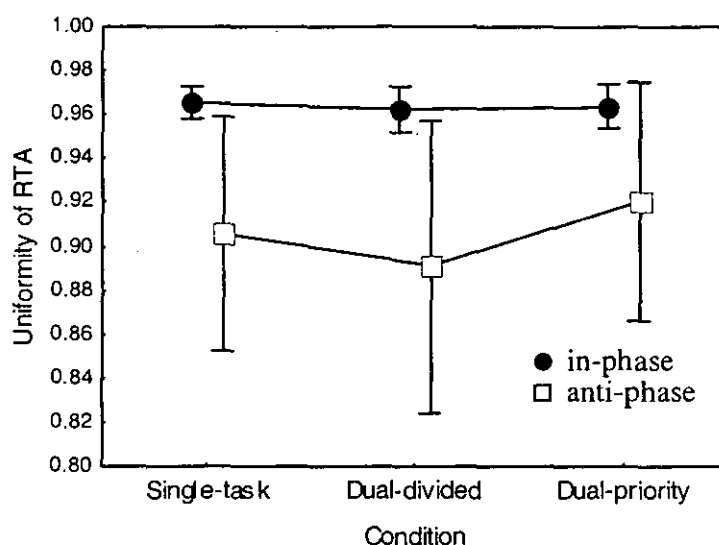


Figure 16. Mean uniformity of RTA for in-phase and anti-phase coordination modes as a function of attention conditions. Error bars represent 95% confidence intervals.

As illustrated in Figure 17A, simple effect analyses of the limb combination  $\times$  coordination mode interaction showed that for in-phase coordination the upper limb combination (0.987) was significantly more stable than both the contralateral (0.947) and ipsilateral (0.956) limb combinations (all  $p < 0.05$ ). For anti-phase coordination, significant differences were observed among all limb combinations (upper = 0.974; contralateral = 0.948; ipsilateral = 0.793, all  $p < 0.05$ ). Comparisons between the coordination modes for each limb combination showed that the in-phase coordination mode was more stable than the anti-phase mode for the upper limb  $t(17) = 8.60$ ,  $p < 0.001$ , and ipsilateral,  $t(17) = 5.94$ ,  $p < 0.001$  limb combinations, but not for the coordination of contralateral limbs.

Of particular importance was the lack of a significant influence of attentional prioritisation on the temporal coupling between the hands (AE of RTA), while

temporal coordination stability was affected by attentional prioritisation suggesting some interaction between the two dimensions of performance.

#### 4.4.4 Attentional measure of prioritising interlimb coordination task

*Probe RT.* Analysis of variance yielded significant main effects of limb combination,  $F(2,34) = 5.07, p < 0.05$ , attention,  $F(1.5,26.0) = 115.13, p < 0.001$ , and coordination mode,  $F(1,17) = 11.35, p < 0.01$ . Post-hoc tests indicated that probe RT was significantly faster during upper limb (307 ms) than during both the contralateral (315 ms) and ipsilateral (316 ms) limb combinations. Probe RT was fastest when attention was exclusively dedicated to the single RT task (277 ms), slowest when attention was devoted to coordination in the dual-task condition (344 ms), and intermediate when attention was divided equally between both tasks (317 ms). Reaction time was significantly faster during in-phase coordination (310 ms) than anti-phase coordination (316 ms). Mean probe RT for the in-phase and anti-phase coordination modes are shown in Figure 17B. None of the interactions achieved statistical significance.

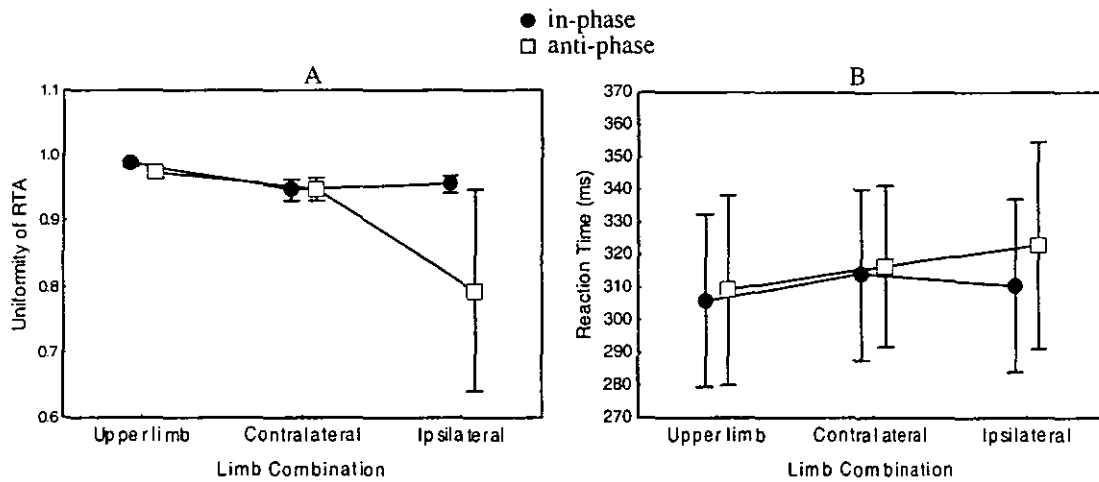


Figure 17. Average performance for in-phase and anti-phase coordination modes as a function of limb combination conditions. (A) Mean uniformity of RTA. (B) Mean vocal RT. Error bars represent 95% confidence intervals.

#### 4.4.5 Structural interference during dual-task performance

As in Experiment 1, a moment-by-moment analysis was performed on the AE of RTA, uniformity of RTA and movement frequency deviation data of each participant (see Temprado et al., 1999). A 3 X 2 X 2 X 4 (Limb Combination X Attention X Coordination Mode X Cycle) ANOVA with repeated measures on all factors was carried out for each dependent variable. The three levels of limb combination were upper limbs, contralateral (left-arm and right leg) and ipsilateral (right-arm and right-leg). Attention consisted of two levels: dual-task with divided attention, and dual-task with priority on the motor task. The two levels of coordination mode were in-phase and anti-phase. The four cycles were -2, -1, +1, +2 – negative and positive values representing the cycles before and after the probe RT stimulus, respectively. Only significant results involving cycle are reported. Complete ANOVA results for each dependent variable are summarised in Table 2.

Table 2. ANOVA Results (*df* and *F* values) for Moment by Moment Analysis for Different Variables (Experiment 2)

	MFD	AE of RTA	UNIF. of RTA
Limb Combination (LC)	$F(2,34) = 0.1$	$F(1.6,28.4) = 35.1^{***}$	$F(1.5,26.6) = 78.7^{***}$
Attention (A)	$F(1,17) = 1.7$	$F(1,17) = 12.7^{**}$	$F(1,17) = 9.5^{**}$
Coordination Mode (CM)	$F(1,17) = 5.16^*$	$F(1,17) = 59.7^{***}$	$F(1,17) = 79.3^{***}$
Cycle (C)	$F(3,51) = 39.1^{***}$	$F(3,51) = 0.0$	$F(3,51) = 0.8$
LC x A	$F(2,34) = 3.4$	$F(2,34) = 2.2$	$F(2,34) = 4.8^*$
LC x CM	$F(2,34) = 1.4$	$F(1.4,24.8) = 16.4^{***}$	$F(1.9,33.2) = 7.3^{**}$
LC x C	$F(6,102) = 1.8$	$F(6,102) = 0.7$	$F(6,102) = 1.3$
A x CM	$F(1,17) = 0.0$	$F(1,17) = 1.3$	$F(1,17) = 0.8$
A x C	$F(3,51) = 1.6$	$F(3,51) = 0.0$	$F(3,51) = 1.3$
CM x C	$F(3,51) = 2.2$	$F(2.7,47.3) = 3.27^*$	$F(3,51) = 1.4$
LC x A x CM	$F(2,34) = 1.2$	$F(2,34) = 1.3$	$F(2,34) = 3.1$
LC x CM x C	$F(6,102) = 0.9$	$F(6,102) = 2.0$	$F(6,102) = 0.7$
LC x A x C	$F(6,102) = 0.6$	$F(6,102) = 0.5$	$F(6,102) = 1.1$
CM x A x C	$F(3,51) = 0.3$	$F(3,51) = 0.3$	$F(3,51) = 0.1$
LC x A x CM x C	$F(6,102) = 1.0$	$F(6,102) = 1.6$	$F(6,102) = 1.9$

\*  $p < 0.05$     \*\*  $p < 0.01$     \*\*\*  $p < 0.001$

*Movement frequency deviation (MFD).* As in the previous study, a main effect of cycle,  $F(3,51) = 39.11$ ,  $p < 0.001$ , illustrated in Figure 18, revealed that movement frequency deviation for the first cycle after the presentation of a stimulus (0.047 Hz) was significantly greater than the remaining cycles (-2 = 0.025; -1 = -0.037 Hz; +2 = 0.005).

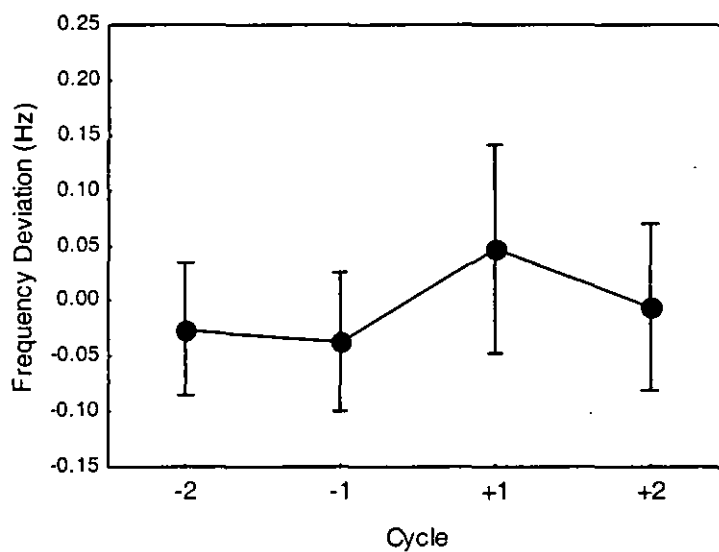


Figure 18. Mean movement frequency deviation across movement cycles before and after probe stimuli. Error bars represent 95% confidence intervals.

*AE of RTA.* There was a significant interaction of coordination mode x cycle,  $F(2.7, 47.3) = 3.27$ ,  $p < 0.05$ . Further examination of the interaction showed no significant changes for AE of RTA across cycles for both in-phase and anti-phase coordination modes (see Figure 19A). However,  $t$ -tests between in-phase and anti-phase modes at each cycle showed that AE of RTA for in-phase coordination mode was significantly smaller than the anti-phase (all  $p < 0.001$ ) across all cycles.

*Uniformity of RTA.* The main effect of cycle was not significant,  $F(3,51) = 0.82$ ,  $p > 0.05$ , nor any of the interactions involving cycle (see Figure 19B).

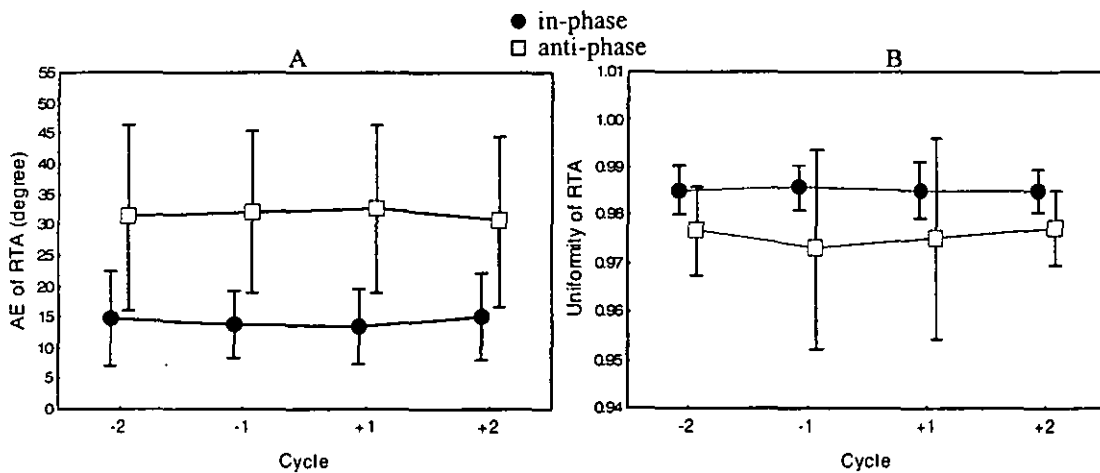


Figure 19. Average performance for in-phase and anti-phase coordination modes across movement cycles before and after probe stimuli. (A) Mean AE of RTA. (B) Mean uniformity of RTA. Error bars represent 95% confidence intervals.

In sum, similar to the results obtained in Experiment 1, the moment-by-moment analysis showed that responses to probe stimuli did not perturb coordination stability or the phase relationship between the hands. In contrast, the probe RT task impacted on the bimanual circle drawing task by increasing the rate of circling for a cycle after presentation of a probe stimulus. Movement frequency returned to the required rate by the second cycle following the probe stimulus.

#### 4.5 Discussion

This study further examined the possible dissociation between the temporal and spatial dimensions of interlimb coordination. In Experiment 1 under attentional prioritisation instructions participants were given performance targets with respect to

the temporal aspects of coordination, in particular the maintenance of the correct phasing between the hands. Under priority instructions the lead-lag between the limbs was reduced and pattern stability was enhanced. In contrast, the circularity and variability of the movement trajectories (i.e., aspect ratio and spatial error) produced by the hands were not affected by attentional focus on the temporal aspects of the coordination task. Experiment 1, therefore, provided evidence of a dissociation between the spatial and temporal dimensions of the circle-drawing task as a result of attentional focus.

In Experiment 2 we sought to further investigate this issue by examining the effects on interlimb coordination of focusing on the spatial aspects of the circle-drawing task. If the temporal and spatial dimensions are specified independently, then directing attention to the movement trajectories produced by the two hands should improve the circularity (i.e., aspect ratio) and stability (i.e., spatial error) of movement trajectories without influencing the temporal aspects of performance. It was also predicted that emphasising the spatial dimension would lead to a reduction in the performance asymmetry commonly observed between the dominant and non-dominant segment during interlimb coordination. The results will be discussed as follows: (a) attentional load associated with the coordination of homologous and non-homologous limb combinations; (b) attentional effects on the inherent asymmetries evident in interlimb coordination (c) dissociating spatial and temporal coupling through the allocation of attention.



#### 4.5.1 Attentional load associated with the coordination of homologous and non-homologous limb combinations.

The first aim of the study was to determine whether there would be a co-variation between attentional load and coordination stability across limb combinations similar to that observed in Experiment 1 where attention was focused on the temporal coupling between the limbs. Previous research (Temprado et al., 2003; Temprado et al., 1999, 2001) employing single-joint bimanual movements has consistently demonstrated that the less stable anti-phase coordination pattern involves a higher central cost (i.e., increased probe RT) to maintain than the more stable in-phase pattern. The co-variation between stability and attentional load was clearly observed in Experiment 1, not only in terms of coordination patterns (i.e., in-phase and anti-phase) but also across limb combinations (i.e., upper, contralateral and ipsilateral).

Although the relationship between coordination stability and central cost across the three limb combinations and coordination modes was not as tight as that observed in Experiment 1, the pattern of results was consistent with the hypothesis of a co-variation between stability and attentional load (cf. Figures 5A,B and 17A,B). At the limb combination level, irrespective of coordination mode, coordination was most stable and responses to probe stimuli were the fastest when the upper limbs performed the circling task followed by the contralateral limb combination with the coordination of ipsilateral limbs showing the least stable coordination pattern and slowest probe RT. With respect to the comparison between coordination modes,

greater central cost was consistently associated with the less stable anti-phase mode when the circling task was performed by the upper limb and ipsilateral limb combinations.

Overall, constraints such as limb combination and coordination mode determined both coordination stability level and central cost regardless of whether attentional focus was on the spatial or temporal dimensions of the interlimb circle drawing task.

#### 4.5.2 Dissociating spatial and temporal coupling through the allocation of attention

Allocation of attention has been shown to be effective in strengthening the temporal coupling between the limbs (Temprado et al., 1999, 2001) (see also Figures 4A,B).

The present study sought to determine whether the spatial aspects of the circle drawing task could be modulated by the attentional prioritisation. The results showed that the circularity (i.e., aspect ratio) of the movement trajectories produced by the two limbs was enhanced by attentional prioritisation to the coordination task in the dual-task situation to a level similar to that observed in the baseline single-task condition. Moreover, the circularity of the trajectories decreased when attention was equally divided between the two tasks (see Figure 12).

With regard to the question of the separability of the temporal and spatial aspects of the bimanual circle drawing task, the results of the two experiments suggest an asymmetry in the relationship between the two components. That is, when attention was directed to the temporal coupling between the limbs (Experiment 1), the

temporal parameters of performance were modulated but not the spatial parameters. In contrast, attentional focus towards the spatial components of the coordination task (Experiment 2) enhanced both the spatial (aspect ratio) and temporal (uniformity of RTA) aspects of performance.

These results suggest that while the temporal dimension of the bimanual circle drawing task can be manipulated without affecting the spatial dimension the reverse situation cannot be achieved. One possible explanation for the observed asymmetry may relate to recent suggestions that the timing of tasks involving continuous movements, such as circle drawing, does not require continuous control from an internal timing system (Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004). That is, in such tasks the temporal properties are emergent and may reflect processes associated with the formation and control of movement trajectories (Semjen, 1996; Zelaznik, Spencer, & Ivry, 2002). Thus, in the present study modulation of the spatial coupling between the limbs would directly influence the temporal coupling between the limbs.

Interestingly, although participants were requested to perform movement trajectories in a consistent fashion the variability of movement trajectories was not modulated by attentional prioritisation. It is possible that focusing attention on the spatial parameters of the two limbs simultaneously imposed some difficulties in monitoring both circularity and variability of movement trajectories, leading participants to concentrate on the ongoing movement trajectory.

#### 4.5.3 Attentional effects on the inherent asymmetries evident in interlimb coordination

The study also aimed to determine whether attentional focus to the spatial components of interlimb circle drawing would reduce or even abolish the performance asymmetries between the limbs. It is well established that the dominant limb (i.e., the right-arm) and the dominant segment (i.e., the arm in the case of coordinating simultaneously the arm and leg) consistently display greater quality of movement trajectories (e.g., movement circularity, circle size) than the non-dominant hand and limb, respectively (Carson et al., 1997; Swinnen et al., 1997).

To our knowledge, the present study is the first to examine whether requiring participants to attend to the spatial components of the circling drawing task, without directing their visual attention to either limb, would improve performance of both limbs simultaneously. The results showed no differences in movement circularity between the limbs for any of the limb combinations (see Figure 14A). Thus, the instruction to focus on the spatial dimension of the interlimb circle drawing task annihilated the previously reported differences between the dominant and non-dominant segments in spatial performance (Swinnen et al., 1997). In Experiment 1, however, where attentional focus was directed to the temporal coupling between the limbs, movement circularity of the dominant segment was consistently superior to the non-dominant segment across all limb combinations (see Figure 11A).

Comparisons of movement circularity of individual limb across limb combinations between Experiment 1 (upper limb: left-hand = 0.903; right-hand = 0.934; contralateral: left-hand = 0.904; right-leg = 0.878; ipsilateral: right-hand = 0.886; right leg = 0.845) and Experiment 2 (upper limb: left-hand = 0.918; right-hand = 0.925; contralateral: left-hand = 0.900; right-leg = 0.899; ipsilateral: right-hand = 0.879; right-leg = 0.857), indicated that movement circularity of the non-dominant segment, in Experiment 2, improved relative to the dominant segment. This suggests that participants may have directed visual attention to the non-dominant segment as a strategy to improve performance of the weaker limb. This view is consistent with previous research (Wuyts et al., 1996) in which specifically directing visual attention to the non-dominant segment reduced the inherent asymmetry between the dominant and non-dominant hand. However, in Wuyts' study improvement in movement circularity of the non-dominant hand affected the performance of the dominant hand compared to when visual attention was directed to the dominant segment or to a neutral position. Of interest in the present study was that the enhancement of movement circularity of the non-dominant segment did not influence movement circularity of the dominant segment. It is possible that proprioceptive information of the non-visually monitored limb may have contributed to maintaining the quality of the movement trajectories, as there is some evidence that this source of information plays an important role in the production of spatial trajectories in the circle drawing task (Verschuere et al., 1999a; Verschueren, Swinnen, Cordo, & Dounskaia, 1999b).

Accordingly, attention appears to constitute a powerful variable that can strengthen both the temporal coupling between the limbs (Temprado et al., 1999, 2001) but also operate at the level of the individual limbs overriding the effect of hand dominance and the biomechanical and neuromuscular constraints that allow the arm to draw circles more skilfully than the foot.

Despite the instruction given to participants to concentrate on movement trajectory and its variability, the results of the present study indicated that the variability of the movement trajectories (i.e., spatial error) produced by the dominant segment was consistently superior to the non-dominant segment across all limb combinations (i.e., upper, contralateral and ipsilateral). Attention, therefore, was not a variable capable of diminishing variability differences between the limbs. Comparing the results of Experiment 1 and 2, the spatial error of the dominant and non-dominant segments across limb combinations were very similar in both experiments. Thus, spatial variability was similar whether attentional focus was on the spatial or temporal components of the circle drawing task.

#### **4.6 Conclusion**

Overall, the interplay between coordination dynamics and the attentional demands incurred by the CNS to maintain coordination patterns across limb combinations was similar regardless of whether attentional focus was given to either the temporal or spatial dimension of the coordination task. In dynamical terms, attention was shown to be powerful source of behavioural information not only to

strengthen temporal coupling between the moving limbs – as previously demonstrated – but also to partially dissociate spatial from temporal coupling. It was demonstrated that attention to the spatial dimension of the coordination task modulated movement trajectories and at the same time the stability of temporal coordination. In Experiment 1 the modulation resulting from attentional focus only occurred in the temporal dimension. A further important finding was that attentional focus on the spatial dimension abolished the inherent performance asymmetries between the limbs. It was speculated that attention may rely on the interaction between proprioceptive and visual information to enhance the quality of movement trajectories.

## **Chapter 5 Literature Review (Part 2)**

Phase 1 of the research program investigated whether the co-variation between coordination stability and central cost observed in bimanual coordination would be evident in the coordination of non-homologous limbs. This research used a dual-task paradigm in which probe RT represented the amount of attentional resources (i.e., central cost) required to maintain performance of a primary interlimb coordination task. In general, performing two unpractised tasks simultaneously will degrade the performance of one or both tasks. It has been common to infer that such degradation is due to competition for limited processing resources. Although a number of recent studies have used brain imaging technology to identify the particular areas of the brain that are active during dual-task performance (e.g., D'esposito et al., 1995; Klingberg, 1998), the precise nature of cortical activity underlying dual-task interference remains unclear. The aim of phase 2 of the research was, therefore, to identify the neural correlates of dual-task performance.

### **5.1 Dual-task Performance: Neurophysiological Basis**

In recent years, there is growing use of neuro-imaging techniques such as functional magnetic resonance imaging (fMRI), positron emission tomography (PET) scan, and magnetoencephalography (MEG) to investigate the neural substrates of dual-task performance. Some studies using fMRI have reported that during dual-task performance, an extra brain area is activated in addition to the areas associated with each task performed alone (e.g., D'esposito et al., 1995; Loose, Kaufmann, Auer, &



Lange, 2003; Schubert & Szameitat, 2003). D'Esposito and colleagues (1995), for example, found that the prefrontal cortex was the brain area additionally activated during a semantic-judgment task concurrently performed with a spatial rotation task. It was suggested that activation of prefrontal cortex was associated with executive functions of coordinating concurrent performance of two tasks. Similar activation of the prefrontal cortex was recently reported during concurrent performance of tasks involving less complex mental operations such as responding to auditory and visual stimuli simultaneously (Loose et al., 2003).

Other studies, rather than finding activation of additional brain areas during dual-task performance, have found overlapping activity in different cortical areas of the cortex (e.g., Adcock, Constable, Gore, & Goldman-Rakic, 2000; Bunge, Klingberg, Jacobsen, & Gabrieli, 2000; Klingberg, 1998; Klingberg & Roland, 1997). That is, if the areas of the cortex activated by task A overlap with the cortical areas activated by task B, then the tasks will interfere when performed together. Klingberg (1998), for example, showed that simultaneous performance of visual and auditory working memory tasks activated (regional cerebral blood flow, rCBF) overlapping parts of the cortex in the dorsolateral prefrontal, inferior parietal and cingulate cortex. The authors suggested that the overlapping activity of brain areas involved in the two tasks might be the physiological basis for dual-task interference. This view was consistent with a study showing that practice of a movement sequence was associated with a decrease in interference between sequence elements and a decrease in

prefrontal and cingulate brain activity, presumably reflecting a decrease in overlapping activation (Passingham, 1996).

Brain imaging techniques such as PET and fMRI have provided useful insights into which parts of the brain are more active during the performance of a specific task. Little is known, however, about the nature of neural activity during dual-task performance. A method that allows measurement of the modulation of cortical activity is transcranial magnetic stimulation (TMS). This method has been used to explore the physiology of the corticospinal system and to probe the role of different parts of the brain in cognitive processing. In the present research, TMS was used to examine cortical excitability during dual-task performance.

## **5.2 Transcranial Magnetic Stimulation: An Overview**

The high spatial and temporal resolution of TMS (Rothwell, 1997) for stimulating specific brain areas has permitted neurophysiologists to gain further insights in to the neural activity of the stimulated areas. The method consists of delivering a non-invasive and painless brief, high-current pulse through a coil positioned on the scalp. The current generates a perpendicular magnetic field that passes through the scalp to induce an electric field in the cortex parallel but in the opposite direction to the field produced in the coil. Operationally, the electric field affects the membrane potential of nerve cells, thus promoting local depolarisation, firing the neurons in the area surrounding where the coil is placed (for a review see Ilmoniemi, Ruohonen, & Karhu, 1999). The application of single-pulse TMS to the scalp overlying a specific

motor cortical area results in a short latency motor evoked potential (MEP) in the target muscle of the limb contralateral to the stimulation. Single-pulse TMS consists of delivering current pulses with a repetition rate lower than 1 Hz, and is used to measure central conduction time and excitability of corticospinal pathways (Chen, Yaseen, Cohen, & Hallett, 1998; Ilmoniemi et al., 1999). The magnitude of the evoked potential can be modulated by the excitability of both cortical inputs and spinal motoneurons to which they project (Petersen, Pyndt, & Nielsen, 2003).

It is now well established that, at threshold intensity, TMS predominantly activates the pyramidal cells transynaptically, through excitatory interneuronal elements of the corticospinal tract, producing descending volleys denominated as I-waves (Day et al., 1989; for a review see Rothwell, 1997). I-wave or indirect wave is thought to originate in the motor cortex through activation of corticocortical projections onto corticospinal neurons (Ziemann & Rothwell, 2000). In contrast, transcranial electrical stimulation (TES), a method that is also used to stimulate the motor cortex, activates directly the pyramidal tract at the initial segment of the neuron, or at proximal internodes in the subcortical white matter, producing descending volleys called D-waves (i.e., direct wave) (Patton & Amassian, 1954; for a review see Rothwell, 1997). In this respect, TMS effects are more sensitive to cortical excitability changes. Threshold intensity is defined as the lowest TMS intensity that evokes a small MEP of at least 50  $\mu$ V. At higher intensities of stimulation, however, TMS and TES may activate corticospinal neurons directly and interneurons transynaptically. The D- and I-wave hypothesis is now widely accepted

for the hand (Nakamura, Kitagawa, Kawaguchi, & Tsuji, 1996) and leg areas (Terao et al., 2000).

Factors such as stimulation intensity, coil position and coil type influence the recruitment of D- and I-waves of the hand and leg area. Werhahn and colleagues (1994), for instance, found that placement of the coil on a parasagittal line over the hand area inducing current in the brain flowing in a postero-anterior direction activated corticospinal fibres transsynaptically. In contrast, when the same coil was positioned on a transverse line over the same hand area inducing current in the brain flowing in a latero-medial direction corticospinal fibres were activated directly. Other factors that influence the focality of the stimulated brain area are shape and size of the coil (Ilmoniemi et al., 1999). The most popular coil shapes are either a figure of eight or a circular coil. The figure of eight, largely used to examine corticospinal excitability of the hand area, is the most focal coil generating current at the intersection of two round connected elements. The field induced by a circular coil is more diffuse and less strong than the figure of eight (Ilmoniemi et al., 1999). There is also a coil, the double-cone, specifically designed to induce an electric field in deeper parts of the brain such as the leg area (Terao et al., 2000; Terao et al., 1994). This coil consists of two round elements connected at an angle of 90° to 100°. Induced current flowing in a posterior to anterior direction has been shown to be the optimal orientation for stimulating the leg motor area with the double cone coil. With respect to coil size, smaller coils can induce stronger and more focal currents than large coils

because of a larger concentration of the magnetic flux in the small coil (Sack & Linden, 2003).

TMS is a powerful tool for studying the physiology of the corticospinal system. It is a relatively new technique capable of providing information on the topographic and temporal organisation of cognitive and motor processes (Jahanshahi & Rothwell, 2000). To our knowledge, TMS has not previously been used to investigate the neural mechanisms involved in dual-task performance. Of specific interest in the present research, was to examine changes in the excitability of the motor cortex associated with responses to probe stimuli in a RT secondary task. The identification of the neural mechanisms underlying dual-task performance deterioration through this technique will provide a significant contribution to the understanding of human cognitive processes.

### **5.3 Bimanual Coordination: An Exemplar Model System**

The attention demands of tasks requiring cyclic coordinated movements have recently been the subject of a number of studies (Temprado & Laurent, 2004; Temprado et al., 1999, 2001). As discussed in Chapters 2 and 3, bimanual coordination stability and attentional demands have been found to strongly co-vary: the most stable pattern was the least expensive for the CNS to perform. The proposal by Temprado and colleagues (for a review see Monno et al., 2002; Temprado et al., 1999, 2001) that attentional cost represents the amount of CNS processing activity required to maintain a particular rhythmical bimanual coordination pattern has also received

support from studies employing brain imaging techniques. Toyokura and colleagues (1999), for example, examined functional cerebral activation (fMRI) in the supplementary motor area (SMA) and sensory motor cortex (SMC) related to in-phase (synchronous opening and closing movements of the two hands) and anti-phase (close one hand while opening the other) coordination modes. The results showed that activity in both SMA and SMC was more pronounced in the bimanual anti-phase mode than the in-phase mode. Greater activation of SMA has also been reported for the anti-phase mode (i.e., non-isodirectional) compared with the in-phase mode (i.e., iso-directional) involving the coordination of the right arm and right foot (Debaere et al., 2001). It has been argued that the greater brain activation for the anti-phase mode is related to the coordination of antagonist muscles (Carson, Riek, & Bawa, 1999; Sadato, Yonekura, Waki, Yamada, & Ishii, 1997; Toyokura et al., 1999).

Analogous findings showing behavioural and functional differences between in-phase and anti-phase coordination modes has come from studies using MEG (magnetoencephalography) (Fuchs et al., 2000; Kelso et al., 1992; Mayville et al., 2001). MEG is a non-invasive method for functional brain mapping that records the associated magnetic field at the scalp from intracellular dendritic current flow in the brain (Kelso et al., 1992). Fuchs and colleagues (2000) explored changes in neural activity patterns of different coordination modes. The experimental task was the coordination of right finger flexion movements with a metronome either between consecutive beats (i.e., syncopated) or on each beat (i.e., synchronised) at frequencies starting from 1.0 Hz to 2.75 Hz in 0.25 Hz incrementing every ten cycles. It was

previously established that a spontaneous behavioural switching from the syncopate mode (i.e., less stable) to the synchronised mode (i.e., more stable) occurs as frequency pacing increases (Kelso et al., 1992). Fuchs and colleagues (2000) found that behavioural differences – relative phase with respect to the auditory metronome – between the two coordination modes (i.e., syncopated and synchronised) were reflected in the functional organisation of neural networks. As such, the syncopated mode was associated with greater activation of SMC areas than the synchronised mode. This result is consistent with the view that the less stable coordination mode (i.e., syncopated mode) requires more attentional demands (Temprado et al., 1999, 2001).

Imaging studies, therefore, have shown that changes in neural connectivity between sensory and motor areas that were directly linked to behavioural changes. The main assumption of this relationship is that the combined activity of billions of neurons and thousands of synapses directly reflect the formation and change of a coordination pattern (Kelso, 1995). Of particular interest in the present research was to examine whether attentional demand differences between in-phase and anti-phase coordination modes would be reflected in changes to corticospinal excitability.

## Chapter 6 Neural Correlates of Dual-Task Performance

### 6.1 Motor Cortical Excitability During Dual-Task Performance

It was recently demonstrated through a dual-task paradigm that attentional demands incurred by the CNS performing a coordination pattern are directly associated with coordination pattern stability (e.g., Temprado & Laurent, 2004; Temprado et al., 1999). Employing a continuous bimanual pronation-supination movement as a primary task and a discrete probe RT as a secondary task (i.e., performed with feet or thumbs), Temprado and colleagues demonstrated that the more stable coordination mode (i.e., in-phase) was the least 'expensive' to perform for the CNS. Structural interference between the probe RT and bimanual coordination tasks was also observed in these studies (Temprado et al., 1999, 2001). More specifically, a detailed analysis of bimanual coordination performance showed that the less stable coordination task (i.e., anti-phase) was briefly disrupted at the moment of the response to probe stimuli.

It has been proposed that interference between functionally proximal areas of the cerebral cortex increases with the degree to which these areas are connected (Kinsbourne & Hicks, 1978). The cortical representations of muscles, for instance, are not discretely located nor sequentially ordered but overlap extensively (Schieber & Hibbard, 1993). Thus, in the dual-task situation elevation of the level of drive required to execute a motor coordinated action may increase the degree of interference between neural centres engaged in a secondary probe RT task (Carson,



Chua, Byblow, Poon, & Smethurst, 1999). The functional meaning of interference between two neural areas engaged in a dual-task performance, however, is not well understood.

Employing a similar dual-task paradigm to that employed by Temprado and colleagues (1999; 2001), a bimanual pronation-supination task was combined with a probe RT task performed with the right foot. TMS was delivered to the foot area of the motor cortex during the probe RT interval to measure the excitability of corticospinal pathway during dual-task performance. It is well established that a monotonic increase in the excitability of the corticospinal pathways occurs during RT responses (see Sommer, Classen, Cohen, & Hallett, 2001). This effect appears to be mediated, at least in part, by a decrease in intra-cortical inhibition (Reynolds & Ashby, 1999). Such inhibitory mechanisms may reflect an adaptive process that increases the sensitivity of the corticospinal pathway to the forthcoming voluntary movement (Hasbroucq, Kaneko, Akamatsu, & Possamai, 1997). What is not clear is whether the co-variation between coordination stability and probe RT would be reflected in corticospinal excitability changes.

## **6.2 Experiment 3**

The purpose of the present study was to examine corticospinal excitability changes in the interval prior to responses to probe RT stimuli during a bimanual coordination task. As coordination pattern stability co-varies with attentional demands (Temprado

et al., 1999, 2001), it was expected that corticospinal excitability would be higher during the anti-phase mode than the in-phase mode.

## 6.3 Method

### 6.3.1 Participants

Ten neurologically healthy volunteers [8 women, 2 men, aged 21 – 38 (mean 27.5 years)], from the University of Tasmania participated in the experiment. All participants self-reported as being right-handed and right-footed, with the exception of one participant being left-handed and left-footed. Approval of the University's Ethics Committee was obtained and written informed consent was obtained prior to participation in the study. Participants were screened for contraindications to TMS prior to participation (see Appendix 2 for screening questionnaire).

### 6.3.2 Task and apparatus

*TMS*: single-pulse TMS was delivered from a Magstim Model 200 stimulator. The surface electromyography (EMG) was recorded via cup electrodes filled with conducting gel fixed with adhesive tape over the right tibialis anterior muscle (TA). The ground reference electrode was placed on the lateral malleolus. Signals were band-pass filtered (10-300 Hz), and amplified (gain 1000-2000) by a Grass Model 12 amplifier. EMG data were sampled at 2000 Hz by a 12 BIT A/D converter (DATAQ system). The centre of a double cone-coil was held on the scalp in the optimal position (i.e., usually 1 cm posterior to Cz and slightly left of the midline) to elicit responses in the right tibialis anterior (TA) at rest. The double-cone coil was oriented

to induce current flowing in a posterior to anterior direction in the brain. The optimal position for evoking MEPs in the right TA was established and marked on the scalp. Resting motor threshold was determined when responses of  $> 50\mu\text{V}$  were evoked in three out of five consecutive stimuli. Intensity of stimulation for experimental trials required eliciting MEPs of  $200\mu\text{V}$  (~5-10% above the individual rest threshold). During threshold determination and subsequent trials, EMG signals were directly monitored through an oscilloscope by the experimenter. To ensure that the coil was maintained at the correct position on the scalp, MEPs at the threshold stimulus intensity were obtained before each trial. Data were stored on disk for offline analysis.

*Reaction Time:* With the right foot resting comfortably on a footswitch, participants responded to randomly presented visual stimuli as quickly as possible by dorsi-flexing the right foot. Visual stimuli consisted of a pair of flashing light emitting diodes (LEDs) mounted on an 8X4 cm box that was placed in front of participants.

*Coordination tasks:* The coordination task consisted of a continuous bimanual task requiring forearm pronation-supination movements. Two modes of coordination were examined: (a) the in-phase mode, in which the forearms are moved together in a mirror-symmetrical manner toward and away from the body midline; (b) and the anti-phase mode, one forearm is rotated towards the body midline (pronation) as the other limb is rotated away from the midline (supination). Custom-built manipulanda were used to record pronation and supination movements of the forearms. Linear

potentiometers located coaxially with the centre of rotation of each manipulanda (length 18 cm, diameter 2 cm) provided continuous transduction of angular displacements. Output voltage signals from each manipulanda were sampled at 2000 Hz by a 12 BIT A/D converter (DATAQ system). The manipulanda were fixed to a table in front of the participant and adjusted for a comfortable seating position. Auditory pacing signals (80 ms, 1000 Hz) generated by a custom-built I/O board, controlled by a standard PC, were presented via loudspeakers.

*Dual-task methodology:* The dual-task paradigm involved the concurrent performance of a rhythmic bimanual coordination task and a discrete reaction time (RT) task. Seven visual probe stimuli were randomly presented in each trial with a minimum inter-probe interval of 4 seconds.

### 6.3.3 Procedure

The experiment was conducted over four sessions and consisted of probe RT and coordination task trials with and without TMS. In the first session, a series of 20 visual stimuli – without TMS – was presented to determine each participant's average RT. Participants were instructed to respond to a probe stimulus by dorsi-flexing their right foot as fast as possible. The mean RT was then used to establish for each individual eight 25 ms target intervals for TMS delivery during the 200 ms preceding the expected RT. For example, if an individual's mean RT was 300 ms the eight target intervals were: 100, 125, 150, 175, 200, 225, 250, 275.

A series of trials in which TMS was not delivered were also performed. These trials were performed in order to verify whether previous findings for coordination task and probe RT measures (Temprado et al., 1999, 2001) would be replicated in the present study. There were four 40 sec trials performed in each of the following conditions: (1) coordination task alone (i.e., single-task), in-phase; (2) coordination task alone, anti-phase; (3) coordination task (in-phase) + probe RT task (i.e., dual-task); (4) coordination task (anti-phase) + probe RT task.

Trials with TMS involved three different conditions: (1) control, participants were at rest (i.e., although visual probes were presented to participants, they were instructed to ignore the stimuli); (2) probe RT alone (i.e., single-task), participants responded to the visual probe stimuli by dorsi-flexing the right foot; (3) dual-task, participants concurrently performed the bimanual in-phase coordination task and the visual probe RT task; (4) dual-task, participants concurrently performed the bimanual anti-phase coordination task and the visual probe RT task. TMS was delivered to the TA muscle at eight target intervals prior to expected movement onset in response to probe stimuli. On two of the seven probe stimuli in a trial TMS was pseudo-randomly delivered during the probe RT interval. TMS was never delivered during the RT interval of consecutive probe stimuli. Over a total of forty 40 s trials for each condition five TMS induced MEPs were recorded at each of the eight target intervals.

Coordination task (i.e., the in-phase and anti-phase coordination modes) trials were performed at 70% of the critical frequency. Critical frequency was determined by asking participants to perform pronation-supination motions in the anti-phase

coordination mode paced by an auditory metronome starting at a frequency of 1 Hz and increasing in .25 Hz increments every 8 seconds to a maximum of 3 Hz. The frequency at which participants showed signs of coordination instability such as phase wandering, a sudden and brief stopping of the coordination task, or a phase transition from the anti-phase coordination mode to the in-phase mode, was considered the critical frequency.

For the dual-task experimental conditions, participants were instructed that they were to focus attention on the bimanual coordination task (i.e., the primary task), and to maintain the coordination pattern, in-phase or anti-phase, at the metronome frequency throughout the trial. The order of single and dual-task condition was randomised across participants, with the exception that the probe RT task alone without TMS was always performed at the beginning of the first session. At least two familiarisation trials were given to participants for each condition before the commencement of the experiment.

#### 6.3.4 Data reduction and dependent measures

*Movement coordination.* Data were low-pass filtered using a second-order Butterworth dual-pass filter with a cut-off frequency of 8 Hz. Continuous estimates of relative phase (RP) between the displacement of the left and right arms, using circular statistics, were obtained from the instantaneous phase of each signal derived from the Hilbert transform. This measure provides the lead-lag time of one limb in relation to the other in their respective movement cycles, with values of  $0^\circ$  (for the in-phase

mode) and  $180^\circ$  (for the anti-phase mode) indicating perfect synchronisation between the limbs. Absolute error of RP (AE of RP) was used as a measure of performance accuracy. Uniformity, the dispersion of the relative phase angle, was calculated as a measure of RTA variability (Mardia, 1972). Small dispersion of the RP gives a uniformity value close to 1 (i.e., low variability), while maximum dispersion is indicated by a uniformity value of 0 (i.e., high variability). A suitable transformation of the circular variance to the range  $0-\infty$ , permitting the use of inferential statistics based on standard normal theory, is expressed in the following form:

$$s_0 = [-2 \log_e(1 - S_0)]^{0.5}$$

where  $S_0$  is the measure of uniformity in the range 0-1, and  $s_0$  is the transformed uniformity measure (see also Byblow et al., 2000). Untransformed measures of uniformity are reported in the text for clarity.

A custom peak-picking algorithm was used to estimate movement frequency. Deviation of movement frequency was used as a measure of the accuracy with which participants were able to maintain the required movement. Variability of movement frequency was assessed through frequency standard deviation (SD).

*Motor evoked potentials.* A customised program was used to detect and calculate the MEP peak-to-peak amplitude in each trial. MEPs in each target interval were averaged for further statistical analyses. Trials were visually inspected at high resolution using a customised graphic program, and an MEP was discarded if there was EMG activity during 100 ms prior to stimulus presentation. To determine the time course of corticospinal excitability changes, the time between a visual probe

stimulus and an MEP was subtracted from the average premotor RT of that trial, and MEPs were then assigned into 25 ms bins according to when they occurred.

*Reaction time.* Probe RT was defined as the delay between the presentation of a visual signal and the release of the footswitch. To be consistent with MEP data analysis, mean premotor RT was calculated from those responses to probe stimuli (not preceded by a TMS pulse) in trials in which TMS pulses were delivered.

Premotor RT was defined as the time between the presentation of a visual probe signal and the onset of EMG activity in the TA muscle.

### 6.3.5 Statistical analyses

Repeated measures ANOVAs were utilised for each dependent variable. In addition, Huynh-Feldt epsilon corrections were applied, where appropriate, to the degrees of freedom of  $F$  tests to compensate for violation of homogeneity assumptions. Slopes of the linear function of the MEPs across intervals were calculated for each individual and submitted to one-way ANOVA with repeated measures. Significant main effects were examined by Tukey post hoc tests. To be consistent with previous analyses (Experiment 1, and 2), RT as well as premotor RT data of the single-task were randomly distributed into two equal groups to be assigned as single-task baselines for dual-task conditions. The two single-task baseline means for RT and premotor RT did not differ significantly (all  $p > 0.05$ ). Trend analyses were also applied to MEP means across intervals in each experimental condition. A conventional alpha level of 0.05 was adopted to indicate statistical differences between means.



## 6.4 Results

### 6.4.1 Trials without TMS delivery

#### 6.4.1.1 Bimanual coordination and probe RT

To examine whether the dynamics of coordination task performance in trials without TMS were consistent with previous findings (Temprado et al., 1999, 2001), frequency deviation and frequency SD from trials in single and dual-task conditions were submitted to 2 X 2 X 2 (Attention X Coordination mode X Hand) ANOVAs with repeated measures on all factors. The two levels of attention were single-task and dual-task conditions. In-phase and anti-phase were the levels of coordination mode and the two levels of hand were left-hand and right-hand. Furthermore, 2 X 2 (Attention X Coordination mode) ANOVAs with repeated measures on all factors were conducted for AE of RP and uniformity of RP. The levels were the same as described above.

*Movement frequency.* No significant main effects or interactions were found for movement frequency deviation. However, for frequency SD there were main effects of hand,  $F(1,9) = 10.74, p < 0.01$ , and attention,  $F(1,9) = 8.35, p < 0.05$ . Frequency variability was significantly higher for the left-hand (0.07 Hz) than the right-hand (0.06 Hz) and was significantly higher for dual-task conditions (0.08 Hz) than single-task conditions (0.05), respectively.

*Absolute error of RP.* There was only a significant main effect of coordination mode,  $F(1,9) = 5.70$ ,  $p < 0.05$ , with the in-phase coordination mode ( $5.05^\circ$ ) showing significantly greater accuracy than the anti-phase mode ( $9.11^\circ$ ).

*Uniformity of RP.* There were only significant main effects of attention,  $F(1,9) = 17.07$ ,  $p < 0.01$ , and coordination mode,  $F(1,9) = 54.87$ ,  $p < 0.001$ . As in previous findings, the in-phase coordination mode (0.985) was more stable than the anti-phase mode (0.964). Coordination task performance in the single-task conditions (0.980) was more stable than in the dual-task conditions (0.970).

*Probe RT.* A 2 X 2 (Condition X Coordination Mode) ANOVA with repeated measures was carried out on the mean probe RT. The two levels of condition were single-task and dual-task. In-phase and anti-phase were the two levels of coordination mode. There were significant main effects of condition,  $F(1,9) = 18.67$ ,  $p < 0.01$ , and coordination mode,  $F(1,9) = 5.37$ ,  $p < 0.05$ . As expected, responses to probe RT were faster in the single-task (229 ms) than in the dual-task (283 ms) condition. Furthermore, responses to probe RT were faster during the in-phase mode (250 ms) than during the anti-phase mode (261 ms).

The results of the present study are consistent with previous findings (e.g., Carson et al., 1997). The non-dominant hand showed greater movement frequency variability than the dominant hand. Performing the coordination task alone was more stable than performing the coordination task simultaneously with a probe RT task (Temprado et al., 1999, 2001). Importantly, the expected relationship between coordination stability and probe RT measures was observed (Temprado et al., 1999,

2001), with the more stable coordination mode being associated with lower central cost.

*Moment-by-moment analysis.* A moment-by-moment analysis was performed on the movement frequency deviation, AE of RP and uniformity of RP in trials without TMS. The analysis consisted of inspecting movement coordination performance cycle-by-cycle to examine the extent to which the response to probe task stimuli interfered with the motor coordination task. A movement cycle was defined as starting from the point where the manipulanda were positioned when the probe occurred to the next end point of pronation-supination motion and the return of the manipulanda to the point where the probe occurred. Six cycles were calculated, three cycles before and three cycles after the occurrence of a probe stimulus. A 2 X 6 (Coordination mode X Cycle) ANOVA with repeated measures on both factors was conducted on the AE of RP and uniformity of RP measures and a 2 X 2 X 6 (Hand X Coordination mode X Cycle) ANOVA on the frequency deviation measure. The two levels of coordination mode were in-phase and anti-phase. The six cycles were -3, -2, -1, +1, +2, and +3 with negative and positive values representing the cycles before and after the probe stimulus, respectively. Additionally, for frequency deviation the two levels for hand were non-dominant and dominant.

*Movement frequency deviation.* There was a significant main effect of cycle,  $F(2.2,20.4) = 8.59, p < 0.001$ , and a coordination mode  $\times$  cycle interaction,  $F(3.6,32.8) = 3.91, p < 0.01$  (see Figure 20). Subsequent analyses indicated that for both in-phase and anti-phase patterns, deviation from the required movement frequency increased significantly for the first cycle after the probe stimulus compared to the remaining cycles (all  $p < 0.001$ ). Furthermore, frequency deviation for the first cycle after the probe stimulus was significantly greater in the in-phase coordination mode than in the anti-phase mode,  $t(9) = 1.46, p < 0.05$ .

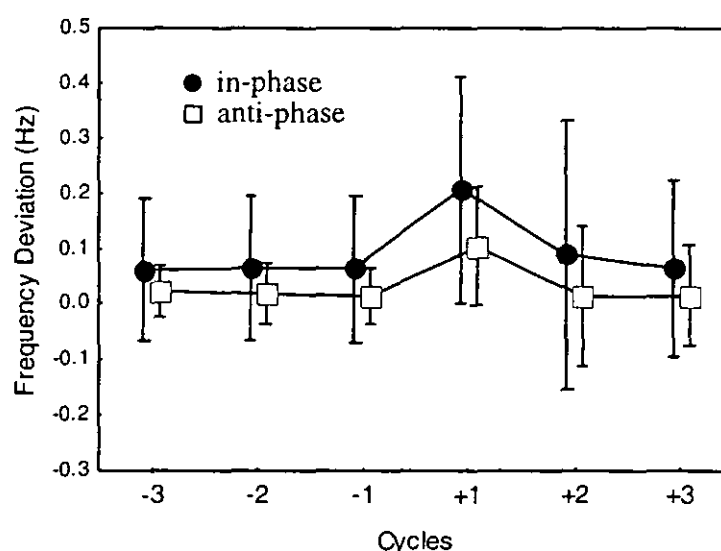


Figure 20. Mean movement frequency deviation for in-phase and anti-phase coordination modes across cycles before and after probe stimuli. Error bars represent 95% confidence intervals.

*Absolute Error of RP.* There were significant main effects of coordination mode,  $F(1,9) = 12.50, p < 0.01$ , and cycle,  $F(2.2,20.2) = 3.39, p < 0.05$ , as well as their interaction,  $F(2.3,21.1) = 3.42, p < 0.05$ . As illustrated in Figure 21A, accuracy

of relative phase was consistently greater across cycles for in-phase coordination than anti-phase coordination. While there was no significant difference across cycles for the in-phase pattern, for the anti-phase pattern the second cycle after the probe stimulus differed significantly from the first three cycles before the probe stimulus (all  $p < 0.05$ ).

*Uniformity of RP.* There were significant main effects of coordination mode,  $F(1,9) = 83.33$ ,  $p < 0.001$ , and cycle,  $F(2.4,22.0) = 3.52$ ,  $p < 0.01$ , as well as their interaction,  $F(4.2,38.1) = 3.31$ ,  $p < 0.05$ . The stability of the in-phase coordination mode was significantly greater than for the anti-phase mode and consistent across cycles (see Figure 21B). However, responses to probe stimuli during anti-phase coordination caused a significant increase in relative phase variability in the first and second cycles after the probe stimulus compared to the second and first cycles before the probe stimulus (all  $p < 0.05$ ). No differences across cycles were detected for the in-phase mode.

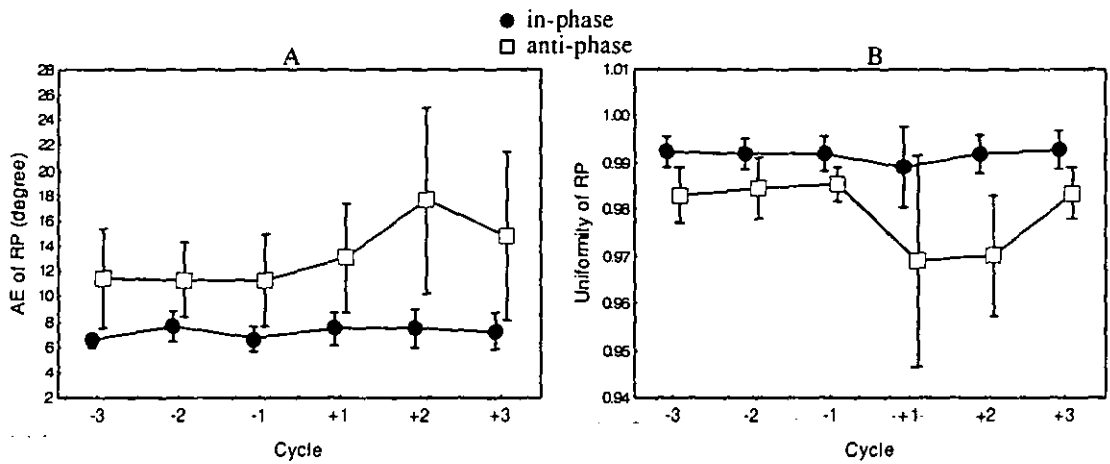


Figure 21. Average performance for in-phase and anti-phase coordination modes across cycles before and after probe stimuli. (A) AE of RP. (B) Uniformity of RP. Error bars represent 95% confidence intervals.

The moment-by-moment analyses, therefore, showed that responses to probe stimuli did not affect coordination task performance in the in-phase coordination mode, but severely disrupted performance of the anti-phase pattern. Responses to probe stimuli, however, did produce momentary increases in the frequency of movement oscillations in both coordination modes. Typical changes in movement displacements resulting from response to probe stimuli during the in-phase and anti-phase coordination modes of a representative subject are shown in Figures 22 and 23.

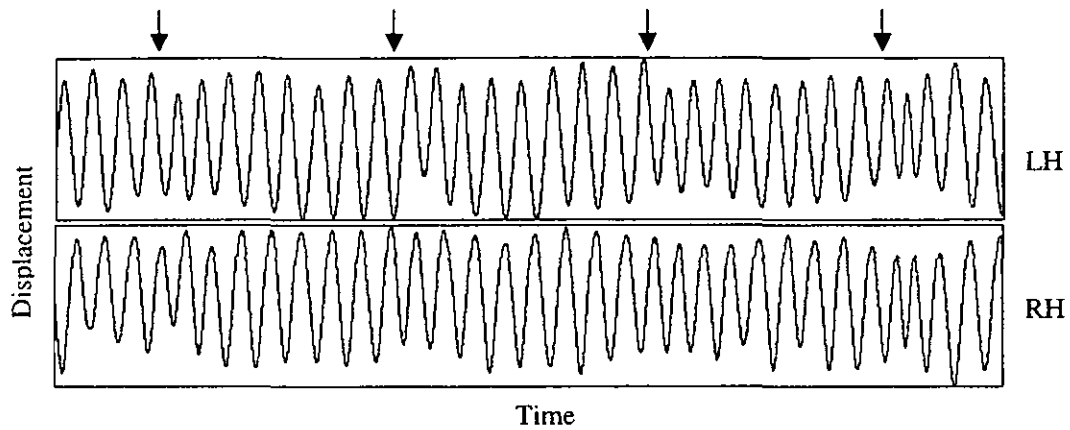


Figure 22. Sample of time series of typical trials in dual-task condition for in-phase coordination mode. Arrows indicate probe stimuli during a trial.

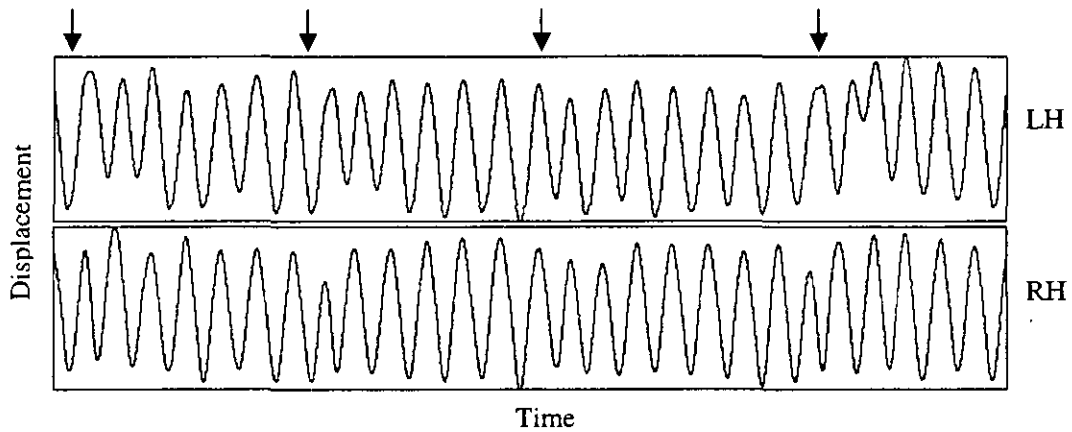


Figure 23. Sample of time series of typical trials in dual-task condition for anti-phase coordination mode. Arrows indicate probe stimuli during a trial.

#### 6.4.2 Trials with TMS delivery

##### 6.4.2.1 MEP amplitude during probe RT interval

MEP amplitude means were submitted to a 3 (condition) X 6 (interval) ANOVA with repeated measures on both factors. The three levels for condition were single task (i.e., probe RT alone), dual-task in-phase, and dual-task anti-phase. The six levels for interval (i.e., time before movement onset) were -150, -125, -100, -75, -50, and -25 ms. As few subjects had MEPs in the -175 and -200 ms bins, these data were combined with the -150 ms interval. Also, as a few subjects had MEPs after the mean

premotor RT (i.e., latency greater than 0), but without EMG activity before the MEP, these data were pooled with the -25 ms interval bin.

ANOVA revealed significant main effects of condition,  $F(1.6, 14.5) = 22.82$ ,  $p < 0.001$ , and interval,  $F(1.9, 17.3) = 114.32$ ,  $p < 0.001$  as well as their interaction,  $F(7.8, 70.5) = 3.50$ ,  $p < 0.01$  (Figure 24). Further examination by trend analysis of the single-task condition showed that MEP amplitude as a function of interval had significant linear and quadratic components,  $F(1, 9) = 64.23$ ,  $p < 0.001$ , and  $F(1, 9) = 57.48$ ,  $p < 0.001$ , respectively. In contrast, both dual-task in-phase and anti-phase conditions showed only significant linear components,  $F(1, 9) = 80.36$ ,  $p < 0.001$ , and  $F(1, 9) = 67.87$ ,  $p < 0.001$ , respectively. A further 2 (coordination mode) X 6 (interval) ANOVA conducted to explore differences between the dual-task conditions across response interval showed only a main effect of interval,  $F(3.8, 34.8) = 69.48$ ,  $p < 0.001$ . The effect of coordination mode,  $F(1, 9) = 1.69$ ,  $p > 0.05$ , and coordination mode x interval interaction did not reach significance level,  $F(5, 45) = 1.03$ ,  $p > 0.05$ .



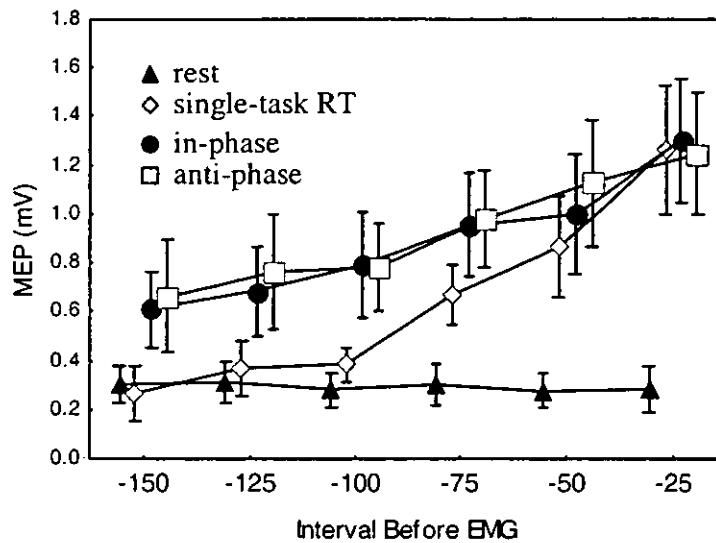


Figure 24. Mean MEP amplitude for single-task (i.e., only RT task), dual-task in-phase, and dual-task anti-phase conditions across time intervals before response initiation. Error bars represent 95% confidence intervals.

A one-way ANOVA performed on the slopes of the MEP functions indicated a significant effect across experimental conditions (i.e., probe RT alone, dual-task in-phase, dual-task anti-phase),  $F(1.7, 15.5) = 5.17$ ,  $p < 0.05$ , with the slope of the probe RT alone condition significantly steeper than both dual-task conditions, which did not differ.

As can be seen in Figure 24, MEP amplitude was approximately equivalent across conditions at the closest interval before movement onset (i.e., -25 ms). A one-way ANOVA showed no main effect across conditions at the -25 ms interval (i.e., single-task RT, dual in-phase and dual anti-phase),  $F(2, 18) = 0.19$ ,  $p > 0.05$ . A further one-way ANOVA was then performed on MEP amplitude means at -150 ms to determine whether the experimental conditions (rest, single-task RT, dual-task in-phase and dual-task anti-phase) differed significantly at the earliest time interval. The interval bins of the rest condition were combined and included in this analysis. There

was no significant difference between the interval bins in the rest condition,  $F(5, 45) = 0.65$ ,  $p > 0.05$ . The ANOVA across all conditions revealed significant differences between conditions,  $F(1.4, 13.4) = 14.13$ ,  $p < 0.001$ , with both dual-task conditions exhibiting significantly higher MEP amplitudes than the single-task (i.e., probe RT alone) and the control (i.e., rest) conditions (all  $p < 0.01$ ). No significant differences were detected between single-task RT and rest conditions or between the dual-task in-phase and anti-phase conditions (see Figure 25).

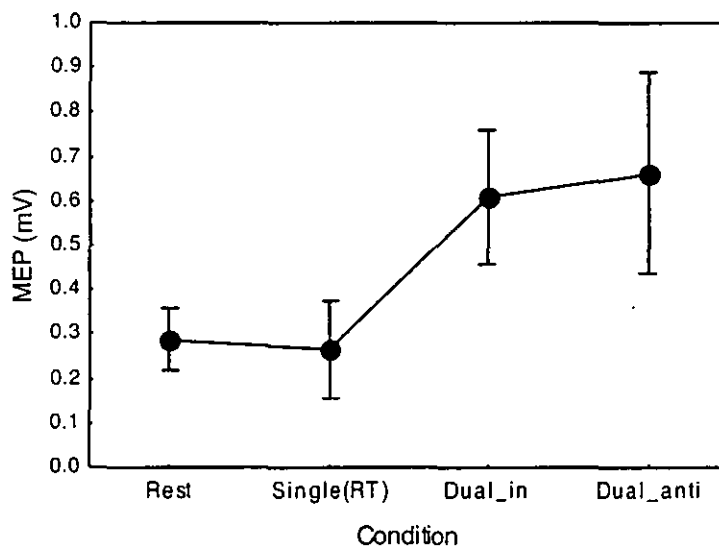


Figure 25. Mean MEP amplitude for control (i.e., rest), single-task (i.e., only RT task), dual-task in-phase, and dual-task anti-phase at the earliest time interval (-150 ms). Error bars represent 95% confidence intervals.

#### 6.4.3 Probe RT in trials with TMS

To be consistent with the MEP data analysis where the time course of MEPs were re-aligned according to mean premotor RT of that trial, premotor RT was used as a measure of RT in trials with TMS. In trials in which TMS was delivered following

some probe stimuli, a 2 X 2 ANOVA with repeated measures were conducted on premotor RT for probe responses that were not preceded by TMS. The two levels of condition were single-task and dual-task. The two levels of coordination mode were in-phase and anti-phase coordination modes.

*Premotor RT.* There were significant effects of condition,  $F(1,9) = 27.62, p < 0.001$ , coordination mode,  $F(1,9) = 8.85, p < 0.05$ , as well as their interaction,  $F(1,9) = 6.90, p < 0.05$  (see Figure 26). Post hoc tests of the significant interaction showed that mean premotor RT in the dual-task in-phase (210 ms) differed significantly from the dual-task anti-phase (219 ms,  $p < 0.05$ ). Overall, premotor RT in the single-task (182 ms) was significantly faster than the dual-task (214 ms) condition.

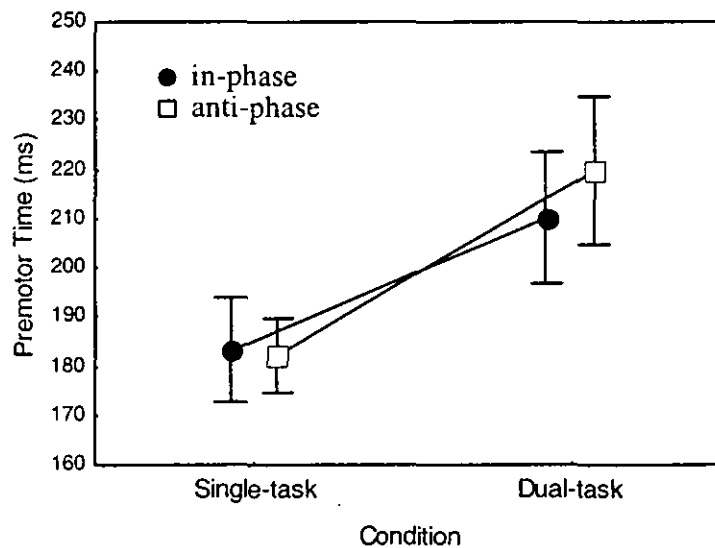


Figure 26. Mean premotor RT for single-task and dual-task conditions in the in-phase and anti-phase coordination modes. Error bars represent 95% confidence intervals.

*Summary.* Of particular importance was the significant difference observed between MEP amplitudes in the rest and probe RT alone conditions and the two dual-

task conditions at -150 ms before response movement onset (see Figure 25). Although MEP amplitudes were higher in the dual-task conditions the slope across response intervals was shallower than that displayed in the single-task (i.e., probe RT alone) condition. Furthermore, MEP amplitudes did not differ between in-phase and anti-phase patterns.

## 6.5 Discussion

It is well established that performing one task is easier and less attention demanding than performing two or more tasks simultaneously (Temprado et al., 1999, 2001). Furthermore, it was shown within a dual-task procedure that coordination pattern stability co-varies with central cost. The greater the pattern stability the lower the central processing activity needed to produce the pattern. An innovative feature of the present study was the investigation of the corticospinal excitability changes during dual-task performance. To address this issue, motor cortical excitability was examined during dual-task performance involving a primary continuous bimanual pronation-supination movement in the in-phase and anti-phase modes while responding to visual probe stimuli.

### 6.5.1 Co-variation between coordination dynamics and central processing activity

Results of the present study related to the dynamics of the bimanual coordination task and its co-variation with probe RT (i.e., trials without TMS) were consistent with previous studies by Temprado and colleagues (1999; 2001). Specifically, coordination was more stable during single-task than dual-task performance; the in-

phase pattern was more stable than the anti-phase pattern; and probe RT was faster during single-task than during dual-task conditions. Furthermore, probe RT also co-varied with the stability of the coordination pattern. As in previous research, responses to probe stimuli did not affect the coupling between the hands of the in-phase coordination mode, but it did disrupt the coordination pattern of the anti-phase mode. This finding is consistent with previous research showing that the stronger the coupling between the hands the weaker the structural interference (Temprado et al., 2001).

#### 6.5.2 Corticospinal excitability in the baseline probe RT task

In the present study, as illustrated in Figure 24, the rise in corticospinal excitability during the response interval in the probe RT single-task trials began at 100 ms preceding movement onset. This is consistent with previous studies (Chen et al., 1998; Leocani, Cohen, Wassermann, Ikoma, & Hallett, 2000) examining the time course of corticospinal excitability of thumb movements across different RT tasks (e.g., simple RT and choice RT). Possible mechanisms underlying the MEP amplitude increase before movement initiation may relate to the interaction between facilitatory and inhibitory systems. Studies with paired-pulse TMS have shown decreased activity of intracortical inhibition during movement preparation (Reynolds & Ashby, 1999). This change in intracortical inhibition, however, occurred in the agonist muscle but not the antagonist muscle. The decreased intracortical inhibition is probably of cortical origin of the agonist facilitation. MEP facilitation preceding

movement, therefore, reflects overall cortical excitation. The MEP amplitude profile obtained in the probe RT (i.e., single-task) condition using a foot response is consistent with the time course of corticospinal excitability reported previously in studies using a hand response.

### 6.5.3 Corticospinal excitability during bimanual coordination

Of particular interest in the present study was the time course of corticospinal excitability during the probe RT interval while performing the primary bimanual coordination task (i.e., dual-task) in the in-phase and anti-phase coordination modes. As the less stable mode of bimanual coordination (i.e., anti-phase) required more attentional demands as reflected in probe RTs, it was expected that the time course of corticospinal excitability would differ between the two coordination modes. Previous research has shown increased brain activity during anti-phase coordination compared to in-phase coordination (e.g., Toyokura et al., 1999). The MEP amplitude profiles in the present study, however, were similar for the in-phase and anti-phase patterns during the premotor RT period both at the earliest time interval (i.e., -150 ms) and in the rate of corticospinal excitability changes during the time prior to movement onset (see Figure 24).

Although probe premotor RT co-varied with coordination stability, MEP amplitudes of the remote muscle (i.e., the tibialis anterior) did not reflect the differential stability between the in-phase mode and anti-phase mode. It is possible that in some measure corticospinal excitability of arm and hand areas differed

between the in-phase and anti-phase modes, but these differences were not large enough to affect the corticospinal excitability of the distant muscle.

#### 6.5.4 Corticospinal excitability during dual-task performance

It was also of interest in the present study to examine whether the MEP amplitude profile evident when the probe RT task was performed alone (i.e., single-task) would differ from the profiles evident when the probe RT task was performed concurrently with the bimanual coordination task (i.e., dual-task in-phase and anti-phase).

In the present study, as illustrated in Figure 24, the rate of increase in MEP amplitude as a function of time was different between single (i.e., probe RT alone) and dual-task conditions (i.e., in-phase and anti-phase). Specifically, the slope was steeper in the probe RT alone condition than in either dual-task condition. Although the slopes differed between single- and dual-task conditions, MEP amplitudes in the interval immediately preceding movement onset (i.e., -25 ms) did not differ significantly among the three conditions (i.e., probe RT alone, dual-task in-phase and anti-phase). It is well established that during premotor RT period there is a monotonic increase in MEP amplitudes indicating an increase of corticospinal excitability before movement onset (e.g., Chen et al., 1998). In that study, Chen and colleagues showed that MEP amplitudes measured both in the self-paced and simple RT tasks were constant at the time interval just before EMG activity. This result suggests that a threshold level of corticospinal excitability is reached prior to movement onset. This phenomenon may account for the invariant MEP amplitude at -25 ms in the present

study. The threshold excitability at –25 ms combined with the increased MEP amplitude at –150 ms in the dual-task conditions would explain the shallower slope relative to the single-task.

The elevated corticospinal excitability during dual-task conditions may reflect either a general increase accompanying the performance of the two tasks at the same time (i.e., a dual-task effect) or a specific activation of corticomotor neurons associated with the upper limbs elevating excitability of neurons controlling the tibialis anterior (i.e., motor effect). In fact, connections between these different segments through the propriospinal neuronal system linking the cervical and lumbar portions of the spinal cord (for a review see Dietz, 2004) suggest that changes in excitability of corticospinal pathways may occur downstream of the motor cortex. However, there is evidence that modulation of corticospinal excitability of a quiescent limb by an active limb may occur at a cortical level. Kujirai and colleagues (1993), for example, reported that MEPs from the hand area were modulated when a conditioning stimulus was delivered to the foot area of the motor cortex, and vice-versa. A more recent study (Sohn & Hallett, 2004) has shown that a brief movement of the leg involving the tibialis anterior had a strong influence on the MEP modulation of a muscle from the hand (i.e., abductor digiti minimi). It was argued that such strong influence is due to a greater physiological coupling of the extremities.



## **6.6 Experiment 4**

The previous experiment showed that, irrespective of coordination mode, MEP amplitude was elevated for dual-task conditions compared with the single probe RT task. At a behavioural level, probe RT responses were faster during single-task performance than during dual-task performance. It was suggested that the elevation in corticospinal excitability during concurrent task performance might either represent dual-task related activity or an influence of the elevation of corticospinal excitability from the upper limbs on the foot area. As Experiment 3 did not include a condition in which corticospinal excitability was measured during the execution of the bimanual coordination task as a single-task, it is not possible to distinguish between the two explanations. In Experiment 4, therefore, MEPs were measured during single-task performance of the bimanual coordination task. It was predicted that if the increase in corticospinal excitability reflected dual-task interference, then MEP amplitude would be greater in the dual-task than the single-task condition. In contrast, if the increase in corticospinal excitability were solely a consequence of neuronal activation of the upper limbs, then no differences between single- and dual-task performance would be predicted.

## **6.7 Method**

### **6.7.1 Participants**

Ten volunteers [8 women, 2 men, aged 23 – 42 (mean 34.9 years)], from the University of Tasmania participated in the experiment. Eight participants were self-

reporting as right-handed and right-footed, and two participants as left-handed and left-footed. None of the participants had previous experience with the task. Approval of the University's Ethics Committee was obtained for the study and written informed consent was obtained prior to participation.

#### 6.7.2 Apparatus and Task

A similar set up and procedure to experiment 3 was utilised in the present experiment with the following changes: (a) as previous findings (Temprado et al., 1999, 2001) were replicated in Experiment 3, coordination task trials without TMS were not included; (b) a bimanual coordination task alone condition was included in trials with TMS to determine whether the increase in MEP amplitudes during dual-task performance previously observed was purely a motor effect, reflecting the motor cortical excitability associated with performing the bimanual coordination task; (c) as MEP amplitude did not differ between probe RT alone (i.e., single-task) and at rest, probe RT alone (i.e., single-task) condition was not included; and (d) to control the point of TMS delivery across participants, TMS pulses were delivered simultaneously with visual probe presentation instead of at different target intervals.

#### 6.7.3 Procedure

The experiment was carried out in one session involving five different conditions: (a) control, participants were at rest; (b) coordination task alone (i.e., single-task), participants performed the coordination task in both the in-phase and anti-phase coordination modes; (c) dual-task, participants concurrently performed the bimanual

coordination task (i.e., in-phase and anti-phase) and a visual probe RT task. In both the rest and coordination task alone conditions the visual probe stimuli were presented but were ignored by the participants.

For all conditions, TMS was delivered simultaneously with the presentation of a visual probe stimulus for two of the seven probe stimuli per trial. Bimanual coordination modes (i.e., in-phase and anti-phase patterns) were performed at 70% of the critical frequency (see Experiment 3 for the procedure used to determine critical frequency). Five trials were performed in each condition with the order of conditions randomised across participants.

#### 6.7.4 Data reduction and statistical analysis

Data were reduced and analysed in the same manner as in the previous experiment (see experiment 3).

### 6.8 Results

#### 6.8.1 MEP amplitude

In order to examine whether there was difference between coordination modes (i.e., in-phase vs. anti-phase) MEP amplitude means were first submitted to a 2 X 2 (Condition X Coordination Mode) ANOVA with repeated measures on both factors. The two levels for condition were single-task and dual-task. There was only a significant main effect of condition,  $F(1,9) = 20.80$ ,  $p < 0.01$ , with the single-task condition (0.602 mV) showing a lower mean MEP amplitude than the dual-task conditions (0.777 mV). The main effect of coordination mode and the condition by

coordination mode interaction did not reach statistical significance,  $F(1,9) = 0.02$ ,  $p > 0.05$ , and  $F(1,9) = 0.07$ ,  $p > 0.05$ , respectively.

Differences in MEP amplitude means among the conditions tested in the present study [i.e., rest, coordination task alone (i.e., single-task) and dual-task], were examined by a repeated measures one-way ANOVA. As the previous analysis did not detect any difference between the coordination modes, data were collapsed across coordination modes. There was a significant effect of condition,  $F(1.6,14.6) = 19.39$ ,  $p < 0.001$  (see Figure 27). Post hoc tests showed significant differences between the rest (0.386 mV) and both the single-task (0.602 mV) and dual-task conditions (0.777 mV), and between the single-task and dual-task conditions (all  $p < 0.05$ ).

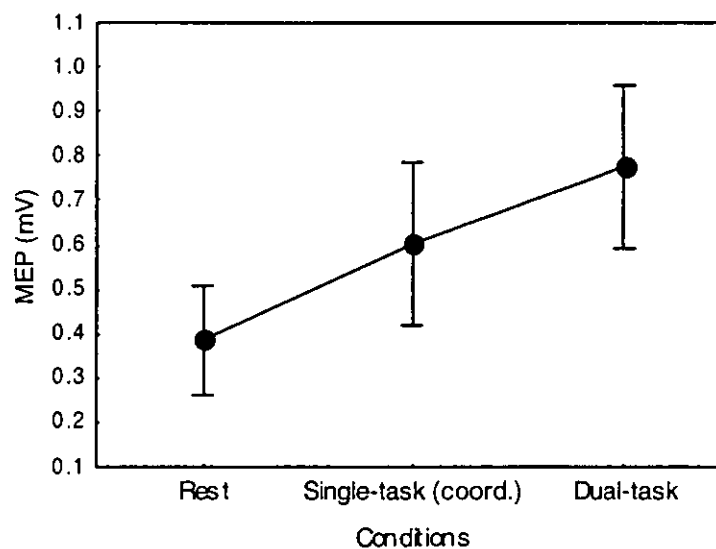


Figure 27. Mean MEP amplitude for rest, single-task (i.e., bimanual coordination), and dual-task (i.e., bimanual coordination + probe RT). Error bars represent 95% confidence intervals.

Thus, the results of the present study confirmed the finding of Experiment 3 that MEP amplitude is not influenced by primary task coordination mode. Of particular importance was the finding that MEP amplitude in the TA (i.e., Tibialis Anterior) muscle during dual-task performance (i.e., bimanual coordination + probe RT task) was significantly elevated compared to performance of the single-task (i.e., bimanual coordination task alone).

#### 6.8.2 Premotor RT

Premotor RT in the in-phase coordination (237 ms) was significantly faster than in the anti-phase mode (255 ms),  $t(9) = -2.74, p < 0.05$ .

### 6.9 Discussion

The results obtained in Experiment 4 showed that MEP amplitudes were elevated when the bimanual coordination task was performed compared to a control condition (i.e., at rest). However, a further increase in MEP amplitudes was observed in the dual-task condition when the bimanual coordination task was performed concurrently with the probe RT task. Thus there appears to be a dual-task effect on cortical excitability over and above the effect produced when movements of the upper limbs were performed.

#### 6.10 Experiment 5

One interpretation of the enhanced corticospinal excitability observed during dual-task performance in Experiment 3 and 4 is that it was a result of structural interference between two motor tasks (i.e., bimanual coordination and responses to

probe stimuli) and as such it might represent a neural correlate of dual-task structural interference. The aim of Experiment 5 was to further investigate this hypothesis by examining corticospinal excitability during dual-task performance involving a non-motor primary task. If facilitation of corticospinal excitability reflects a general neural correlate of dual-task interference, then elevated corticospinal excitability should occur irrespective of the nature of dual-task. If, however, the elevated excitability evident in Experiments 3 and 4 reflects specific structural interference between two motor tasks then differences between the two dual-task conditions would be predicted.

## **6.11 Method**

### **6.11.1 Participants**

Ten volunteers [9 female, 1 male, aged 18 – 40 years (mean 22.1 years)], from the University of Tasmania participated in the experiment. None of the participants had been involved in previous experiments. Eight participants self-declared as right-handed and right-footed and two as left-hand and left-footed. Approval of the University's Ethics Committee was obtained for the study and written informed consent was gained prior to participation.

### **6.11.2 Apparatus and tasks**

A similar methodology and procedure to Experiment 4 was utilised in the present study with the following changes: (a) as MEP amplitudes did not differ between dual-task in-phase and anti-phase conditions in the previous experiments, only the dual-

task anti-phase condition was examined; (b) probe RT alone (i.e., single-task) was performed as the baseline condition; and (c) a dual-task condition was included in which a cognitive tone-counting task was performed concurrently with the visual probe RT task. In the cognitive task, participants heard a series of randomly presented high (2000 Hz) and low pitch (1000 Hz) tones and had to keep count of the number of high-pitched tones presented in that trial. Thirteen to nineteen tones of each pitch were administered in each trial.

#### 6.11.3 Procedure

The experiment was carried out in one session involving three different conditions: (a) control (i.e., probe RT alone), participants responded to visual probe stimuli by dorsi-flexing the right foot; (b) motor dual-task, participants concurrently performed the bimanual coordination task in the anti-phase mode with the visual probe RT task; (c) cognitive dual-task, participants concurrently performed the cognitive tone counting task, with the visual probe RT task. For all conditions, TMS was delivered simultaneously with the visual probe RT stimulus on two of the seven probe stimuli presented each trial. The anti-phase pattern was performed at 70% of the critical frequency (see experiment 3 for the procedure of finding critical frequency). Five trials were collected for each condition with the order of conditions randomised across subjects.

#### 6.11.4 Data reduction and statistical analysis

Data were reduced and analysed in the same manner as in the previous experiments (see Experiment 3).

### 6.12 Results

To examine differences among conditions, each dependent variable (i.e., MEP amplitude and premotor RT) was submitted to one-way repeated measures ANOVAs. The conditions were single-task (i.e., probe RT alone), motor dual-task (i.e., anti-phase coordination mode and probe RT), and cognitive dual-task (tone counting and probe RT). As in Experiment 3 and 4, only premotor RTs not preceded by TMS were considered for statistical analysis.

#### 6.12.1 MEP amplitude

The ANOVA revealed a significant effect among conditions,  $F(1.3, 12.5) = 20.29$ ,  $p < 0.001$ . Post hoc tests showed that the MEP amplitudes in the motor dual-task (0.946 mV) condition were significantly higher than in the probe RT alone (0.393 mV) and cognitive dual-task (0.530 mV) conditions (all  $p < 0.001$ ), which did not differ from each other (see Figure 28A).

#### 6.12.2 Premotor RT

The ANOVA yielded a significant effect among conditions,  $F(2, 18) = 61.55$ ,  $p < 0.001$ . Post hoc tests showed that all conditions differed significantly from each other (see Figure 28B) with the probe RT alone condition showing the fastest premotor RT



(173 ms), the cognitive dual task the slowest (320 ms), and the motor dual-task (235 ms) displaying an intermediate premotor RT (all  $p < 0.001$ ).

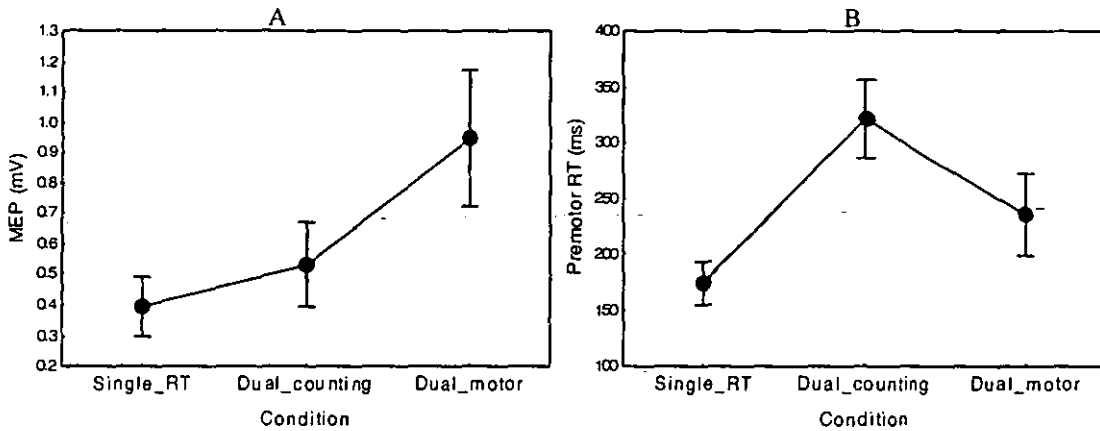


Figure 28. Mean MEP amplitude (A) and mean premotor RT (B) for single-task (i.e., RT alone), cognitive dual-task (i.e., counting tone task), and motor dual-task (i.e., bimanual coordination) conditions. Error bars represent 95% confidence intervals.

### 6.13 Discussion

The aim of this study was to examine whether the increased motor cortical excitability seen in dual-task situations involving a primary motor coordination task and a secondary discrete probe RT task would also be evident in the concurrent performance of a non-motor cognitive task and the probe RT task. The results clearly showed that when the primary task was non-motor (i.e., counting tones) cortical excitability did not increase to the same extent as when the primary task was a continuous motor task (bimanual coordination). Conversely, attentional demands as measured by probe RT were significantly higher for the tone-counting than the bimanual coordination task.

## 6.14 General discussion

In the second phase of this research, three experiments were conducted to explore the neural correlates of dual-task interference during bimanual in-phase and anti-phase coordination modes. To specifically address this issue, corticospinal excitability was assessed during dual-task performance. Experiment 3 examined the time course of changes in motor cortical excitability in the premotor RT interval to secondary probe task stimuli during single-task (i.e., probe RT alone) and dual-task conditions (i.e., bimanual in-phase and anti-phase coordination tasks + probe RT). Experiment 4 examined whether the enhanced corticospinal excitability during dual-task performance seen in Experiment 3 was a motor effect rather than reflecting a general dual-task effect. Finally, Experiment 5 examined corticospinal excitability during dual-task performance involving either a motor primary task (i.e., bimanual coordination) or a non-motor (tone-counting) primary task.

Experiment 3 showed that corticospinal excitability just prior to EMG onset (i.e., -25 ms) reached similar peak levels across all conditions (i.e., single-task or dual-task). It is suggested that this threshold level reflected partial activation of neuronal elements in a system in which neural activities spread to excite output neurons of the cortex (Wickens, Hyland, & Anson, 1994). Consistent with the results of the present study, Chen and colleagues (1998) reported similar peak levels for corticospinal excitability just before EMG onset for simple RT and self-paced discrete movement tasks.

In contrast, corticospinal excitability at the interval (i.e., -150 ms) well before EMG onset was more elevated in the dual-task condition, irrespective of coordination mode, than during single-task (i.e., probe RT alone) performance. As expected, responses to probe task stimuli were faster in the single-task condition than the dual-task conditions. From the results of Experiment 3, however, it was not possible to distinguish whether the increase of corticospinal excitability reflected a general dual-task related neural activity or an effect of corticomotor excitability of the upper limbs onto the TA motor cortical area.

In Experiment 4 the issue of whether the elevated corticospinal excitability evident during dual-task, but not single-task (i.e., probe RT alone), was due to effects of activation of the upper limb cortical areas was examined. The results gave partial support to the hypothesis. That is, corticospinal excitability was elevated when the bimanual coordination task was performed and MEPs were measured in the relaxed TA muscle compared to a control rest condition (i.e., no motor activity). However, when both tasks (bimanual coordination + probe RT) were performed concurrently, corticospinal excitability was significantly higher than when only the coordination task was performed. This finding indicates that while the motor cortical excitability of neural populations related to movements of the upper limbs may influence the excitability of neuronal elements representing the tibialis anterior, it does not explain the elevated MEPs evident during dual-task performance.

If two tasks use one or several identical overlapping fields of the cerebral cortex (Roland & Zilles, 1998) or functional proximal areas (Kinsbourne & Hicks,

1978), then the two tasks cannot be performed simultaneously without interference. Elevated corticospinal excitability during dual-task performance in the present research therefore appears to reflect the degree of response competition between cortical representations of the neuromuscular systems engaged in the primary and secondary tasks. Although the target muscle for TMS was quiescent, there is evidence that neuronal activities related to movement preparation are occurring in the motor cortex prior to movement onset (Georgopoulos, 1991; Kalaska, Crammond, Cohen, M., & Hyde, 1991).

Brain imaging studies have been providing valuable information with respect to the cortical structures engaged in dual-task performance (Klingberg, 1998; Klingberg & Roland, 1997). Of particular relevance is the finding that the neurophysiological changes evident during dual-task performance are directly associated with behavioural measures of dual-task interference. Klingberg (1998), for example, showed that dual-task interference, reflected in deteriorated RT responses, was associated not only with a more pronounced brain activation during dual-task than single-task performance but also with the activation of overlapping parts of the cortex. Although in the present research, it was not possible to assess the degree of overlapping activation of the brain areas, the TMS procedure did demonstrate that elevated corticospinal excitability was associated with delayed RT responses when the concurrent performance of two motor tasks was required. If the elevated corticomotor excitability reflects a general neural correlate of dual-task interference that is associated with delayed probe RT, then it would be expected that elevated

corticomotor excitability would also be evident in dual-task situations that do not involve a motor primary task.

To test this prediction in Experiment 5 corticospinal excitability was also examined in a dual-task situation involving a non-motor primary task (i.e., tone-counting) and the secondary probe RT task used in Experiments 3 and 4. The results showed that corticospinal excitability was elevated for the motor dual-task (i.e., bimanual coordination + probe RT) condition, as in the previous studies, but not for the cognitive dual-task or baseline (i.e., rest) conditions. With respect to the probe RT task, RT was significantly slower in the cognitive dual-task condition than the motor dual-task condition. These results, therefore, did not support the view that the elevation of corticospinal excitability might reflect a general neural correlate of dual-task performance. Rather, the effect appears to be specific to the concurrent performance of two tasks with conflicting motor components (i.e., cyclical arm movements and discrete foot responses).

It was assumed in the present study that structural interference did not occur during dual-task performance involving the non-motor primary task, as there was no overt response. If probe RT reflects resource allocation, then it can be concluded that the primary tone-counting task was more attentional demanding than bimanual coordination task. Previous studies have shown that a tone-counting task similar to that employed in the present study (i.e., counting low- or high-pitched tones) dramatically slowed RT to visual stimuli during a sequential RT task (Hsiao & Reber, 2001; Rah, Reber, & Hsiao, 2000). Hsiao and Reber (2001) proposed that there is a

limited-capacity working memory and that the capabilities of this system were reduced when participants engaged in a secondary tone-counting task. It was recently shown that a tone-counting task involved activation of several brain regions including the putamen, cerebellum and anterior cingulate, parietal and dorsolateral prefrontal areas (Ortuno et al., 2002). Although the tone-counting task employed by Ortuno and colleagues (2002) consisted of counting a consistent series of tones, it seems reasonable to assume that the counting task used in the present study involved a similar neural network activation.

It may be that dual-task interference evident between tasks that require working memory ability as well as sustained attention may be best described in terms of resource or capacity interference. In neuro-imaging studies, the neural processes associated with the notion of a limited attentional resource in dual-task situations involving working memory components have been associated with an increased activation of cortical areas associated with the secondary task (Adcock et al., 2000; Bunge et al., 2000). In particular, it has been reported that an increase in attentional demand is associated with increased activation of the dorso-lateral prefrontal cortical area. From a psychological point of view, it is assumed that attentional prioritisation during dual-task performance reflects the allocation of attentional resources from a limited capacity system (Temprado et al., 2001; Tsang et al., 1995). It has been demonstrated recently that attentional prioritisation is linked with activity in the prefrontal lobe (Rowe, Friston, Frackowiak, & Passingham, 2002). Specifically, Rowe and colleagues (2002) showed that focusing attention on a finger sequencing

motor task rather than on a visual distractor task enhanced the effective connectivity between the dorsal prefrontal cortex and premotor cortex. Cortical areas of the frontal lobe appear to be critical regions for the allocation of attentional resources.

Interestingly, motor cortex activation related to the motor task was not affected by attentional prioritisation suggesting that resource allocation effects influence structures upstream of the motor cortex.

In the motor dual-task, a relationship between corticospinal excitability changes and responses to probe RT was evident across Experiment 3, 4, and 5. That is, the increase in corticospinal excitability was associated with delayed response to probe RT during motor dual-task when compared with single-task condition. Consistent with Temprado and colleagues (2001), the present results also showed that structural interference occurred in the primary task, at the level of coupling between the limbs. That is, responses to probe stimuli were more disruptive to performance of the anti-phase coordination mode than the more strongly coupled in-phase coordination mode. Examination of the effects of structural interference showed that responses to probe stimuli perturbed momentarily the continuous oscillations of the primary task by speeding up movements of the hands, irrespective of coordination mode. It seems likely that this form of structural interference reflects peripheral factors such as reactions to postural disturbance caused by lifting the foot in response to probe stimuli. Consistent with the hypothesis that the transient increases in the upper limb oscillation rate are manifestations of mechanical perturbation was the finding that such effects were not reduced by attentional prioritisation (see

Experiment 1 and 2). Although Temprado and colleagues (2001) argued that dual-task interference is unidirectional characterised by alterations in the primary task, it is argued that the delay in probe RT during performance of the bimanual coordination task may largely reflect structural interference at the level of the motor cortex. In Experiment 5, the motor dual-task condition showed a smaller increase in probe RT over the single-task condition than the cognitive dual-task, but higher corticospinal excitability. The large difference between the motor and cognitive dual-tasks in probe RT suggests that the central cost of moving the limbs did not reflect activity in neural circuits upstream of the motor cortex. In fact, the basic argument from structural interference models is that dual-task interference that occurs when performing two similar tasks but not requiring the same whereby common mechanisms of processing is that neural interference is modality-specific areas (e.g., Navon & Miller, 1987). That is, the increase in excitability appears to be a characteristic sign of structural interference caused specifically by overlapping of neural activity between the motor cortical areas engaged in the dual-task performance.

### **6.15 Conclusion**

According to Temprado and colleagues (2001), both attentional resource and structural interference accounts are not distinct interpretations of dual-task interference but they can co-exist. The present research further showed that capacity and structural interference accounts may have different neural manifestations. The increase of corticospinal excitability was evident in the motor dual-task performance,



but it was not evident in the cognitive dual-task condition. It is suggested that demands in attentional resource reflect neural activities upstream of the motor cortex, whereas structural interference reflects an overlapping activity of the two motor areas engaged in the dual action.

## **Chapter 7 Summary and Conclusions**

The present research was conducted to investigate attentional processes in interlimb coordination systems. The first part of the literature review described the two most important forms of dual-task interference, capacity and structural. Interference resulting from limited capacity occurs when the attentional demands of performing two tasks simultaneously exceed capacity and performance of one or both tasks is compromised. Structural interference results when two tasks require similar physical or neural structures. As the interlimb coordination system was the experimental model used to explore attentional processes at the behavioural and neurophysiological levels, the following sections described some important properties of interlimb coordination dynamics and the effects of attention on such dynamics. The final sections illustrated some factors that may alter interlimb coordination dynamics as well as the effects of the type of probe RT on coordination dynamics.

The first phase of the research program was conducted to explore whether the finding of a co-variation between attentional demands and bimanual coordination stability would be observed in a different interlimb coordination system involving the coordination of arms and legs (i.e., contralateral and ipsilateral). In the present research two aspects of the experimental strategy were modified from previous studies (Temprado et al., 1999, 2001). First, a task that involved coordination in both spatial and temporal dimensions was employed. In particular, this task (i.e., interlimb circle drawing task) allowed the assessment of the temporal relationship between the

limbs and the performance of precise movement trajectories by each limb. Second, a vocal probe RT was employed to minimise the occurrence of structural interference. There were four main findings from the first two experimental studies. Firstly, attentional cost measured through probe RT co-varied with the stability of coordination patterns for both homologous and non-homologous limb combinations. Secondly, attentional focus selectively dissociated performance between the temporal and spatial dimensions of the interlimb coordination task. Thirdly, attentional focus specifically directed towards the spatial dimension of interlimb coordination (i.e., movement trajectories) reduced the inherent asymmetrical performance between the dominant and non-dominant segment. Lastly, a secondary probe RT task involving vocal responses revealed a type of peripheral structural interference on the coordination task that could not be prevented by attentional prioritisation.

Consistent with previous research (Temprado et al., 1999), the co-variation between coordination pattern stability and attentional cost evident for bimanual coordination was also observed in the coordination of an arm and leg. Differences in the stability of the coordination patterns across limbs were accounted for by constraints (e.g., allocentric, egocentric or muscular homology) that may converge or counteract each other in determining the stability of a coordination pattern (Temprado et al., 2003).

The present research found that spatial and temporal dimensions of interlimb circle-drawing task were not totally independent from each other. Whereas temporal aspects of the coordination could be manipulated through attentional focus without

affecting the spatial aspects, the spatial dimension could not be manipulated without having a modulating effect on the temporal dimension. It was speculated that when participants were instructed to focus on producing perfect circles with the limbs vision was used to monitor one limb at a time with the non-monitored limb relying on proprioceptive information. Such asymmetrical distribution of visual attention may have caused consistent relative phase offsets with a proprioceptive monitoring mechanism triggering corrections to the phase relationship between the limbs when the relative phase offsets exceeded a certain threshold value (Verschueren et al., 1999a).

Attentional focus to the spatial characteristics of individual limbs through instructions to participants to enhance the general spatial performance of both limbs abolished the spontaneous differences between the dominant and non-dominant segments. It was suggested that participants directed visual attention primarily to the non-dominant segment and that the spatial performance of the dominant segment was maintained by proprioceptive information. Attention constitutes a power tool capable of not only strengthening temporal coupling between the limbs but also the spatial characteristics of the task. In practical terms, attention may have a potential use as a strategy in motor rehabilitation as well as in programs designed especially to maintain or enhance the quality of motor capacity in the elderly population.

According to Temprado and colleagues (2001) increasing resource allocation to the coordination task strengthens the coupling between the effectors and reduces the structural interference from the probe RT task. The secondary vocal probe RT

employed in the first two studies did not interfere with the temporal coupling between the limbs, but it did cause a transient increase in the oscillation rate of the limbs (i.e., movement frequency deviation). It was suggested that there are two levels of structural interference: (a) at the cortical level resulting from interactions within the motor cortex; (b) at the peripheral level resulting from the mechanical coupling between motor tasks. The first is a more flexible type of interference, which can be attenuated by the allocation of attention (Temprado et al., 2001). The second, likely to occur from mechanical interactions between effectors, is a more rigid type of structural interference, which cannot be prevented by the allocation of attention.

The second part of the research examined the neural correlates of dual-task interference involving a bimanual forearm pronation-supination task. A literature review described the neurophysiological basis of dual-task performance mainly from studies employing neuro-imaging techniques. As TMS was the procedure used to investigate the neural activity of the motor cortex during dual-task performance, the following section offered an overview of the use of the TMS technique to examine motor cortex excitability. The last section of the review described some recent neurophysiological findings associated with bimanual coordination. Three experimental studies were then described exploring the neural correlates of dual-task interference.

There were three main findings from the experimental studies conducted in the second part of this research. Experiment 1 the corticospinal excitability of the TA (i.e., muscle related to probe RT response) did not differ between the in-phase and

anti-phase coordination modes. However, corticospinal excitability was greater during dual-task performance, irrespective of coordination modes, than during single-task (i.e., probe RT task alone) performance. Experiment 2 showed that the increase in corticospinal excitability during dual-task performance reflected primarily dual-task related activity. In the final experiment the increase in corticospinal excitability occurred during a motor dual-task condition (i.e., primary motor task + probe RT), but not during a cognitive dual-task condition (i.e., primary cognitive task + probe RT).

Since stability of a coordination pattern co-varies with attentional cost (Temprado et al., 2001), it was hypothesised that stability differences between the coordination modes would be reflected in the corticospinal excitability measure. Although coordination pattern stability co-varied with attentional cost the TMS results showed no coordination mode modulation at the corticospinal level. It is possible that the small differences between the coordination modes, at the behavioural level, were not large enough to influence on the excitability of corticospinal pathways. Of particular interest, however, was the large difference in corticospinal excitability between single-task and dual-task performance. It was suggested that the increase in corticospinal excitability during dual-task performance may reflect structural interference related to performing two tasks simultaneously. The final experiment showed, however, that the increased corticospinal excitability was not a general effect of dual-task performance but specific to the concurrent performance of two motor tasks. Elevation of corticospinal excitability, therefore, appears to be a

characteristic sign of structural interference that reflects the degree of overlapping neural activities between the two motor cortical areas engaged in the primary and secondary tasks. It was further suggested that the increase in probe RT in the motor dual-task situation compared to the single-task condition was primarily due to structural interference at the level of the motor cortex, rather than the allocation of attentional resources to the primary task.

In sum, stimulation of the motor cortex appears to be a useful means to assess neural changes during dual-task performance. In particular, this research showed specific neural changes during dual-task involving two motor tasks. However, future research is needed to further examine: (a) changes in corticospinal excitability within the attentional prioritisation procedure; (b) the role of a general inhibitory system in mediating interference when two tasks are performed concurrently; (c) the interaction between structural interference and corticospinal excitability across different probe RT tasks (e.g., foot, finger, vocal).

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## Appendices

**Appendix 1. Adapted Edinburgh Handedness Questionnaire**

Surname:

Given Names:

Date of Birth:

Sex:

Please indicate your preferences in the use of hands and feet in the following activities by answering with R (for right hand or right foot preference) or with L (for left hand or left foot preference).

What hand do you use to write with? \_\_\_\_\_

What hand do you use mostly in everyday tasks, such as:

Tooth brushing? \_\_\_\_\_

Using a spoon to eat? \_\_\_\_\_

Which foot do you prefer to kick with? \_\_\_\_\_

Which foot do you prefer to pick up an object with the toes? \_\_\_\_\_

## Appendix 2. Screening Questionnaire for TMS studies

### MEDICAL HISTORY QUESTIONNAIRE

#### VOLUNTEERS PARTICIPATING IN STUDIES INVOLVING TRANSCRANIAL MAGNETIC STIMULATION

SURNAME:.....

GIVEN NAMES:.....

DATE OF BIRTH:..... SEX:.....

ADDRESS:.....

HOME PHONE:.....

WORK PHONE:.....

#### Please answer the following:

Have you ever had an adverse reaction to TMS?

☐ Yes☐

No

Have you ever had a seizure?

☐ Yes☐

No

Have you ever had a serious head injury (including neurosurgery)

☐ Yes☐

No

Have you ever had any other brain-related condition?

☐ Yes☐ No

Have you ever had any illness that caused brain injury?

☐ Yes☐ No

Have you been told you have hemophilia

☐ Yes☐ No

Have you ever undergone electro-convulsive therapy

☐ Yes☐ No

Have you ever been told that your blood pressure was abnormal?

☐ Yes☐ No

Do you have any metal in your head (outside the mouth)? Such as shrapnel, surgical clips or staple, or fragments from welding or metalwork?

☐ Yes☐

No

Do you have any implanted devices such as cardiac pacemakers, medical pumps, intracardiac lines, cochlear implant, pins, nails, clips, wire, artificial limb or joint?

☐ Yes☐ No



- Do you suffer from frequent or severe headaches? ☐ Yes ☐ No
- Do you have diabetes? ☐ Yes ☐ No
- If yes, how is it controlled? Dietary means...insulin injector...oral medication...uncontrolled....
- Are you taking any medication? ☐ Yes ☐ No
- Is there any possibility you are pregnant? ☐ Yes ☐ No
- Does anyone in your family have epilepsy? ☐ Yes ☐ No
- Do you need further explanation of TMS and its associated risks? ☐ Yes ☐ No

If you answered yes to any of the above, please provide details (use the reverse if necessary):

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I certify that the above information is correct to the best of my knowledge. I have read and understand the entire contents of this form and I have had the opportunity to ask questions regarding the information on this form.

**Participant's name:**

**Participant's signature**

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